

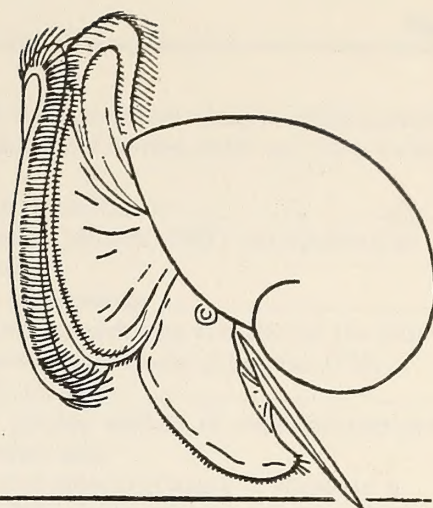


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THE VELIGER

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Volume 24

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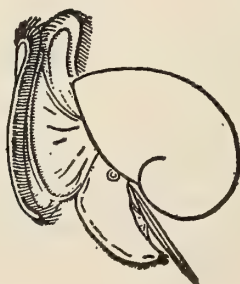
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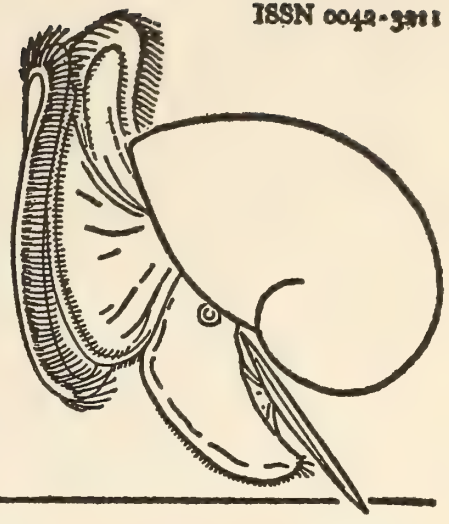


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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
 SUPERFAMILY, FAMILY, Subfamily, Genus, (Subgenus)
New Taxa

A New Species of *Nautilus* from Palau

BY

W. BRUCE SAUNDERS

Department of Geology, Bryn Mawr College, Bryn Mawr, Pennsylvania 19010

(3 Plates; 2 Text figures)

INTRODUCTION

IN 1976, THE DISCOVERY OF *Nautilus* living in deep water outside the fringing reef of Palau, Western Caroline Islands, was briefly highlighted in National Geographic Magazine (DUGDALE & FAULKNER, 1976). The Palauan *Nautilus* have subsequently been the focus of investigations of anatomy, ecology, movement and distribution, involving trapping, study and release of more than 1100 live animals (SAUNDERS, 1981, SAUNDERS *et al.*, 1978; SAUNDERS & SPINOSA, 1978, 1979). Although a considerable body of data concerning the Palauan *Nautilus* has been assembled, precise taxonomic status of this form has been uncertain; it has been variously identified as *Nautilus pompilius* Linnaeus, 1758; *N. cf. pompilius*, and *N. repertus* Iredale, 1944. Systematic comparison of this form with other recognized species of *Nautilus* indicates that the Palauan form deserves separate taxonomic designation; it is here described as a new species, *Nautilus belauensis*.

CEPHALOPODA Cuvier, 1798

ECTOCOCHLIA Schwartz, 1894

NAUTILOIDEA Hyatt in Zittel, 1900

NAUTILIDAE de Blainville, 1835

Nautilus Linnaeus, 1758*Nautilus belauensis* Saunders, spec. nov.

(Figures 2a, 3-14; Tables 1, 2)

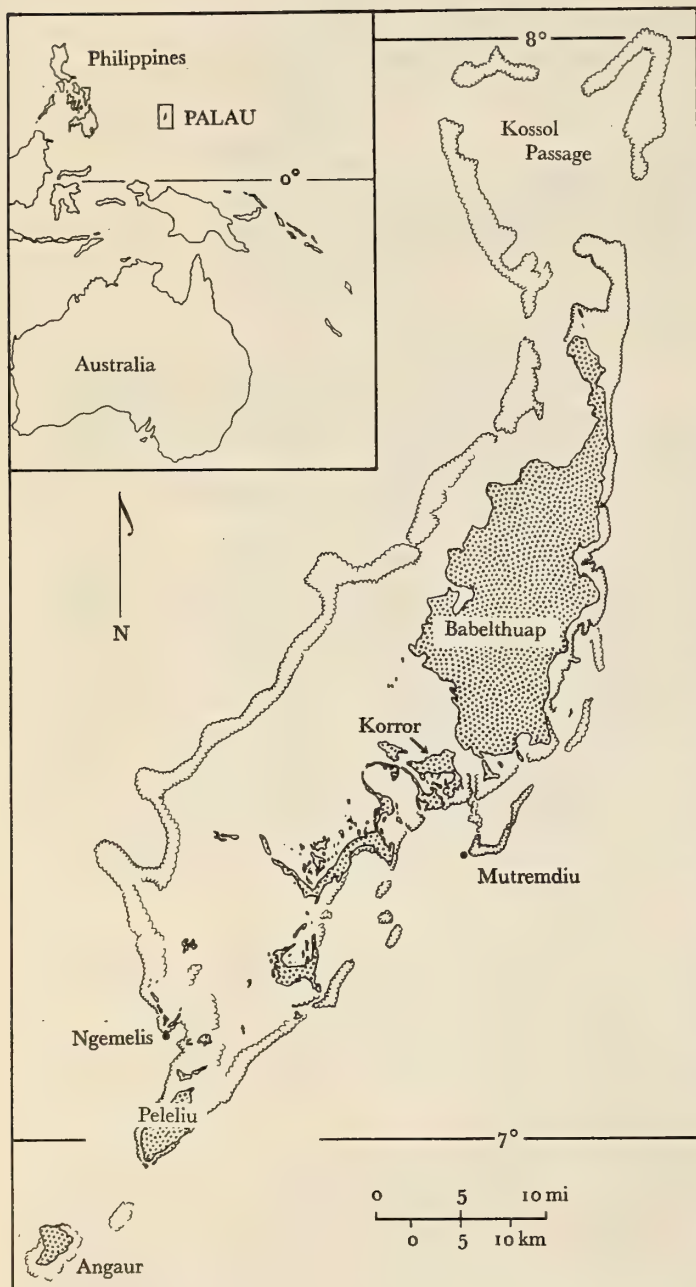
Nautilus sp. Dugdale & Faulkner, 1976.*Nautilus repertus* Iredale, 1944. FAULKNER, 1977; SAUNDERS & WEHMAN, 1977: 86.*Nautilus pompilius* Linnaeus, 1758. FAULKNER, 1976: pls. 118, 119; SAUNDERS & WARD, 1979; CARLSON, 1979.*Nautilus* cf. *N. pompilius* Linnaeus, 1758. SAUNDERS, SPINOSA, TEICHERT & BANKS, 1978: plt 9, figs. 7, 8; plt. 10, fig. 16; text-fig. 6; SAUNDERS & SPINOSA, 1978: figs. 1-11; SAUNDERS & SPINOSA, 1979.

Diagnosis. A species of *Nautilus* similar to *N. pompilius*, but distinguished by its large mature size (mean shell diameter approx. 200 mm), longitudinally crenulate growth lines on the shell and by the wide central radular teeth.

Description. Definition of *Nautilus belauensis* is based upon examination of 1132 animals trapped along the outer fringing reef of Palau, W. Caroline Islands, during 1977-1979 (Figure 1). The holotype (USNM 730549) is a mature male weighing 1450 g (body plus shell weight in air) with a shell diameter of 216 mm. For typological reference, data on additional paratypes and topotypes are tabulated in Table 1.

The new species is unusually large in comparison to other species of *Nautilus* (see SAUNDERS, 1981). Mature shells of 375 animals trapped in 1977 ranged from 180 to 226 mm diameter, with a mean diameter of 204 mm; the weight (body plus shell) of 268 mature animals ranged from 950 to 1800 g, with a mean of 1308 (SAUNDERS & SPINOSA, 1978).

Sexual dimorphism is prominent in mature animals, expressed as differences in overall size and proportions. The mean diameter and total weight of 213 mature males reported by SAUNDERS & SPINOSA (*ibid.*) was 209 mm ($N=213$) and 1426 g ($N=138$) respectively, in contrast to 198 mm ($N=89$) and 1157 g ($N=81$) for mature females. In addition, mature males exhibit a broader aperture (mean 99 mm) than females (mean 91 mm), as a result of constriction of the female aperture as maximum size is approached, at approximately 180 mm diameter (Figures 8, 9). This does not occur in the males, which



require a larger body chamber to accommodate the large accessory reproductive organ, the spadix. It is notable that males substantially outnumber females; of 1132 animals trapped and sexed, 817, or 72%, were male.

As in *Nautilus pompilius*, the umbilicus of *N. belauensis* is small (approximately 5% of the shell diameter) and, with only rare exceptions, it is filled by a calcareous deposit, the callus. Deposition of the callus begins at approximately 100 mm diameter in the Palauan form and it completely closes the umbilicus by 110 mm diameter. The total number of septa in the shell of mature animals varies, but there are commonly 35 (Table 2). As in other species of *Nautilus*, septal approximation (closer spacing of adjacent septa) occurs between the 7th and 8th septa, in association with the nepionic constriction, as well as between the final two septa in many specimens. In addition, the final septum may be thicker than previous septa. Maximum growth is marked by thickening of the aperture, a white body chamber that lacks color banding, deposition of a black layer along the apertural margin, accentuation of the hyponomic and ocular sinuses, and elongation of the body chamber. These features characterize maturity in the sense that maximum growth has been achieved, but their relationship to reproductive maturity is unknown; they may, in fact, be gerontic characters. Approximately 80% of specimens of *N. belauensis* trapped in Palau were mature; by contrast, very young animals (less than 100 mm diameter) were extremely rare: only 5% were less than 160 mm diameter (78% of the mean diameter, 204 mm) and the smallest of 1132 animals trapped measured 85 mm shell diameter (111 g weight in air).

(← adjacent column)

Figure 1

Location map showing principal *Nautilus* trapping sites (Mutremdiu Point and Ngemelis Island) in Palau, West Caroline Islands

Explanation of Figure 3

Nautilus belauensis spec. nov., Palau, West Caroline Islands

Mature female, trapped May, 1977, ca. 200 m depth, Mutremdiu Point, Palau; photographed in shallow water

approx. $\times \frac{1}{4}$



Figure 3

Table 1

Data from type specimens of *Nautilus belauensis* Saunders, spec. nov.

	Spec. No.	Locality	D	U	Wm	Wt	Mat	Sex	Misc.
fig'd	paratype USNM 730672	Palau, W. Caroline Is.	101.7	7*	52.4	170	I	—	umbilicus open
fig'd	paratype USNM 730673	Palau, W. Caroline Is.	211.4	9*	96.5	1462	IBM	M	umbilicus open
fig'd	holotype USNM 730549	Palau, W. Caroline Is.	216	—	103.5	1449	M	M	
	topotype USNM 730674	Palau, W. Caroline Is.	149.7	—	72.4	455	I	F	
	topotype USNM 730534	Palau, W. Caroline Is.	218.8	—	101.7	1543	M	M	
	topotype USNM 730535	Palau, W. Caroline Is.	208.8	—	100	1421	I	M	
	topotype USNM 730536	Palau, W. Caroline Is.	209.5	—	99.8	1443	M	M	
	topotype USNM 730537	Palau, W. Caroline Is.	198.2	—	87.2	—	M	F	
fig'd	topotype USNM 730675	Palau, W. Caroline Is.	215.8	—	106.4	—	M	M	white umbilicus
fig'd	paratype USNM 730676	Palau, W. Caroline Is.	190.	—	85.1	—	M	F	
fig'd	paratype USNM 730546	Palau, W. Caroline Is.	205.3	—	95.5	1238	IBM	F	

D, maximum shell diameter; U, umbilical diameter measured across umbilical shoulders; Wm, maximum width at aperture (all measurements in mm); Wt, weight (gms) of body plus shell in air at time of capture; Mat animal maturity, classed as: M, fully mature, displays all mature characteristics including blackened and thickened aperture, deepened ocular, hyponomic sinuses, white body chamber; MB, barely mature, with aperture barely blackened and thickened; IBM, submature, without apertural blackening or thickening, but with full size, white body chamber; I, immature, shows no characteristics of maturity (for details see Saunders and Spinosa, 1978). Sex determined by sexing of live animals. Asterisked measurements are approximate.

Table 2

Data on size, number of septa, septal thickening and approximation in sectioned shells of mature
Nautilus pompilius, *Nautilus belauensis* sp. nov. and *Nautilus scrobiculatus*

Species	Number	Locality	D	Sex	S	Aprx	Thk
<i>Nautilus pompilius</i> Linnaeus	BMC unnumb.	Philippines?	168.2	—	38	7/8, 14/15, 37/38	38
<i>Nautilus pompilius</i> Linnaeus	BMC unnumb.	Philippines?	172*	—	34	7/8	34
<i>Nautilus pompilius</i> Linnaeus	BMC unnumb.	Philippines?	146	—	29	7/8	28/29
<i>Nautilus pompilius</i> Linnaeus	BMC unnumb.	Philippines?	172.4	—	34	7/8	34
<i>Nautilus pompilius</i> Linnaeus	BMC unnumb.	Philippines?	171*	—	35	7/8	35
<i>Nautilus pompilius</i> Linnaeus	BMC unnumb.	Philippines?	172	—	33	7/8	—
<i>Nautilus pompilius</i> Linnaeus	BMC unnumb.	Philippines?	176*	—	32	7/8	32
<i>Nautilus belauensis</i> sp. nov.	BMC unnumb.	Palau	199.7	F	35	7/8	35
<i>Nautilus belauensis</i> sp. nov.	BMC unnumb.	Palau	215.1	M	35	7/8	34/35
<i>Nautilus belauensis</i> sp. nov.	BMC unnumb.	Palau	219.9	F	35	7/8	34/35
<i>Nautilus belauensis</i> sp. nov.	BMC unnumb.	Palau	214*	M	35	7/8	34/35
<i>Nautilus belauensis</i> sp. nov.	BMC unnumb.	Palau	213*	—	37	7/8	37
<i>Nautilus belauensis</i> sp. nov.	BMC unnumb.	Palau	204.9	F	36	7/8	35/36
<i>Nautilus belauensis</i> sp. nov.	BMC 228	Palau	207.3	M	35	7/8	34/35
<i>Nautilus belauensis</i> sp. nov.	BMC 17	Palau	205.6	M	33	7/8	33
<i>Nautilus scrobiculatus</i> (Lightfoot)	BMC unnumb.	Solomons	192*	—	33	7/8	32/33

D, maximum shell diameter (mm); S, total number of septa at maturity; Aprx, septal approximation, or close spacing between adjacent septa; count begins with first (smallest) septum; Thk, presence of thickened final septum. All specimens fully mature. Asterisked measurements are approximate. BMC prefix indicates collections at Bryn Mawr College.

The shell sculpture of *N. belauensis* is distinctive. In all living species of *Nautilus*, the growth lines are sinuous, reflecting ocular and hyponomic sinuses (Figure 11), but in the Palauan species the shell sculpture includes delicate, longitudinally crenulated ridges that produce a distinctive, concentrically lirate pattern (Figures 5, 7). The lirae are present on all specimens examined (including very young shells). They are most prominently expressed on the ventrolateral portions of the shell and their strength may vary between individuals. This sculpture is known in only one other species of *Nautilus*, *N. scrobiculatus* (see comparison).

The pattern of shell coloration is variable, but characteristically comprises irregular, brown to reddish brown stripes extending from the umbilicus and branching across the flanks. The color bands cover the entire immature shell (Figures 6, 12), but deposition of the bands ceases as maturity is approached, often at approximately the position of the last septum in mature shells. Thus, the final body chamber, or ventral one-half of the mature shell, lacks color bands (presumably a protectively advantageous pattern). In a few specimens, the color bands do not extend to the umbilicus, leaving a white adumbilical region, such as that which has been cited as distinguishing other species, including *Nautilus repertus* and *N. ambiguus* (see SAUNDERS, 1981 for discussion).

Except for the generally larger size, the anatomy of the soft parts appears indistinguishable from *Nautilus pompilius*. In fact, it is curious that no differences in the soft parts of any of the described species of *Nautilus* have been recorded, with the exception of a difference in the hood texture of the single known specimen of *N. scrobiculatus* noted by WILLEY (1902: pl. 78, fig. 3). The jaw apparatus is also indistinguishable, except for its large size, from other species of *Nautilus*; this is a revision of earlier statements to the effect that the jaw of the Palauan *Nautilus* appears to differ from those of *N. pompilius* and *N. macromphalus* (SAUNDERS *et al.*, 1978; and see Discussion).

The radula in mature animals is a formidable structure, measuring approximately 10 mm by 40 mm. As in fossil nautiloids (and in the living species *N. macromphalus* and *N. pompilius*) the radula consists of a series of rows, each comprising 13 elements, including a central rachidian tooth and 4 lateral teeth, 4 attenuate, crescentic marginal teeth and 4 subrectangular marginal support plates (Figure 2; see also SOLEM & RICHARDSON, 1975; SAUNDERS & RICHARDSON, 1979).

Comparison. The large size, the lirate shell sculpture and the wide radular teeth of *Nautilus belauensis* are the primary criteria for distinguishing the new species. With the exception of two large specimens from Australia described as *N. repertus* (see IREDALE, 1944) all other *Nautilus* are considerably smaller, ranging from 140 mm diameter for *N. pompilius* from Fiji, and 170 mm diameter for the same species from the Philippines; 160 mm for *N. macromphalus*, and 180 mm for *N. scrobiculatus*. It is notable that the larger size of *N. belauensis* is more than just a product of a longer period of growth, because (a) the total number of septa are similar in both the Palauan (33-37 septa) and Philippine forms (32-38 septa) in spite of their size differences (Table 2), and (b) umbilical closure occurs at a considerably larger size in *N. belauensis* (at approximately 100 mm diameter) than in Philippine *N. pompilius* (at approximately 75 mm diameter). The prominent longitudinal crenulations on the shell of *N. belauensis* are known only in *N. scrobiculatus*, in which they are coarser and occur in combination with a markedly different shell form (see SAUNDERS, 1981, figure 5). Some faint longitudinal sculpture may occur in occasional specimens of *N. pompilius* and in *N. macromphalus*, but it does not approach the strength characterizing *N. belauensis*. Comparison of the radula of the new species indicates that the central rachidian tooth and to a lesser extent the second lateral teeth are wider and

Explanation of Figures 4 to 9

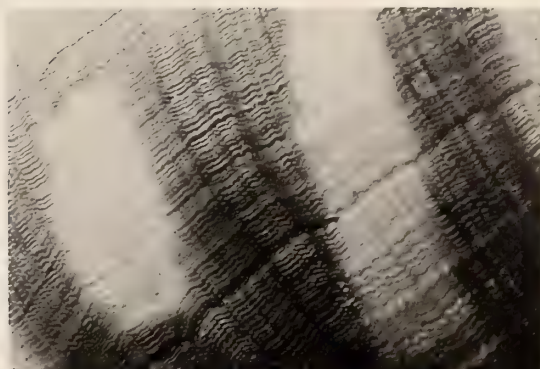
Nautilus belauensis spec. nov., Palau, West Caroline Islands

- Figure 4: Apertural view of swimming female shown in Figure 3 approx. $\times \frac{1}{2}$
 Figure 5: Enlarged view of shell showing longitudinally crenulate shell sculpture (Paratype, USNM 730546) $\times 3\frac{1}{2}$
 Figure 6: Shell of young specimen (Paratype, USNM 730672) caught alive, in which umbilical callus had not yet been deposited. Note presence of color bands on entire shell and shallow ocular sinus $\times \frac{1}{2}$

- Figures 7, 8: Lateral and apertural views of shell of holotype (USNM 730549), a mature male, trapped July 7, 1977, Mutremdiu Point, Palau. Note absence of color bands on body chamber and accentuated ocular sinus; both are characteristic of mature shells $\times \frac{1}{2}$
 Figure 9: Apertural view of mature female (Paratype, USNM 730676) $\times \frac{1}{2}$



4



5



6



7



8



9

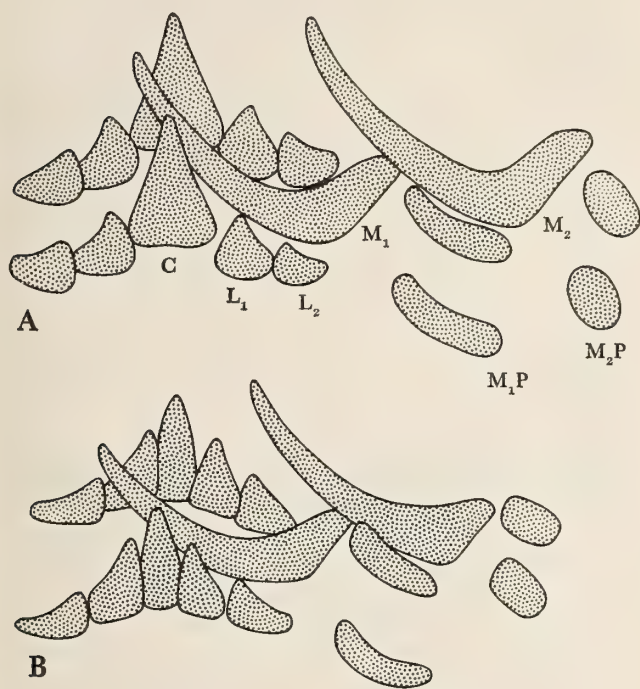


Figure 2

Camera lucida drawings of anterior views of portions of radulae of *Nautilus belauensis* spec. nov. from Palau (A), and *Nautilus pompilius* from Tañon Straits, Philippines (B). C - central rachidian tooth; L_1 , L_2 - first and second lateral teeth; M_1 , M_2 - inner and outer marginal teeth; M_1P , M_2P - inner and outer marginal support plates. Each row includes a total of 13 separate elements, including (1) C, (2) L_1 , (2) L_2 , (2) M_1 , (2) M_2 , (2) M_1P , (2) M_2P . Note the differences between the two species in the proportions of the central rachidian teeth (C).

more broadly triangular than equivalent elements in *N. pompilius* from the Philippines (Figure 2). The maximum width (at the base) of the central rachidian tooth is approximately 65-70% of the height in *N. belauensis*, in contrast to *N. pompilius* from the Philippines, in which W/H is approximately 45-50% (Compare Figures 2a, b).

The Jaw Apparatus. As described elsewhere (SAUNDERS *et al.*, 1978) the jaw apparatus of *Nautilus* differs from that of all other living cephalopods because it includes calcareous elements on the chitinous jaws. In *Nautilus*, there is an arrow-shaped calcite structure (the ryncholite) in the anterior end of the upper jaw, and a denticulated calcite deposit (the conchorhynch), covering the occlusal

surface of the lower jaw. The ryncholite functions as an incisor that articulates against the inner crescentic surface of the conchorhynch, producing a strong shearing action (SAUNDERS *et al.*, *op. cit.*). Ryncholites and conchorhynchs have long been known as fossils, ranging back to Middle Triassic (approx. 210 MYA). In comparing the jaw apparatus of the various living species of *Nautilus*, SAUNDERS *et al.* (*op. cit.*) reported that *N. macromphalus* was distinctive in bearing delicate, highly crenulated ridges across the occlusal surface of the conchorhynch, in contrast to *N. pompilius* from the Philippines, which exhibited straight, low-relief denticles (*ibid.*: plt. 9, figs. 6, 16). It was noted that the conchorhynch of Palauan *Nautilus* (referred to as *N. cf. pompilius*) was close to *N. macromphalus*, but that it was unique in bearing a series of distinctive biserial grooves on the inner surface of the chitinous lower jaw (*ibid.*: plt. 10, fig. 16); they anticipated that this feature of the jaw might be of taxonomic value. However, subsequent examination of large numbers of fresh specimens of *N. belauensis* from Palau, of *N. pompilius* from the Philippines and of *N. macromphalus* from New Caledonia indicates that the differences cited earlier are highly variable and appear to be of little systematic significance. Specifically, chevron-like biserial grooves on the lower jaw do not occur in all specimens of *N. belauensis* from Palau, but they do occur in some Philippine specimens. In addition, the degree of relief and crenulation of the denticles on the surface of the conchorhynch are highly variable. They have been severely abraded in many specimens and in some cases the conchorhynch has been completely worn through, presumably the by-product of a hard-shelled diet. It appears that these elements can be rebuilt by the animal, apparently by precipitation of calcite from the papillary buccal tissue; exact counterparts or molds of the calcareous elements can be seen in the papillary arrangement in fresh material. This is supported by and would explain the presence of mucous cells on the epithelium of the buccal papillae containing granules (FUKUDA, 1980: 28; figs. 4-17). Thus, it is not surprising that the surface of the conchorhynchs of *Nautilus* kept for long periods of time in aquaria and fed on soft foods such as shrimp and fish, exhibit fresh appearing high-relief, delicate crenulations, in contrast to most live-caught animals, in which the calcitic elements are often badly worn.

The function of the radula of *Nautilus* has been regarded as unknown (SOLEM & RICHARDSON, 1975; SAUNDERS *et al.*, 1978). However, observations of live animals from Palau show that the animals extrude the radula in tongue-like fashion while the jaws are open and withdraw it as the jaws close. This is apparently a reflex action that,

in combination with the shape and orientation of the radular teeth, would be highly effective in grasping material, moving it into the mouth and into the esophagus, providing both an aid to biting (in conjunction with the denticulated conchorhynch) and for passing food into the digestive system. No evidence of the radula being used as a rasping device has ever been observed.

Ecology. *Nautilus belauensis* is presently known only from Palau, W. Caroline Islands, where it lives in the fore reef habitat. Animals were caught there in baffle-type traps baited with fish (tuna, snapper, barracuda), suspended on the reef face at approximately 150-300m depths for 3-7 nights. The depth distribution of *Nautilus* appears to be related to temperature. The animal prefers water temperatures between 10° and 20° C, which in Palau occur at depths of approximately 125-200m. The animals will tolerate elevated temperatures for short periods of time, but perish within several days in water warmer than 25° C. However, this would not prevent short term incursions into warm, shallow water, and in 1979, one animal was trapped in Palau at a depth of 70m, where it was presumably foraging in shallower water.

As documented by SAUNDERS & SPINOSA (1979), the animals may range extensively along the reef front. Movement of tagged animals for distances of up to 150km in 332 days and 51 km in 31 days was documented in 1978. Additionally, two animals were recaptured, in 1979, 4km from their release site after a period of 5 days, documenting movement of at least 0.8 km per day. At the same time, however, *Nautilus* may remain at—or periodically return to—the same site for extended periods. Numerous tagged animals have been recaptured at the same sites where they had been released (*ibid.*) and one mature animal (no. 127) that had been released June 23, 1977, at Mutremdiu Point, Palau, was recaptured at the same site on July 3, 1979. This animal was mature when first tagged and released in 1977,

thus establishing that *Nautilus* lives at least two years beyond maturity; a major contrast to typically short-lived dibranchiate cephalopods.

While details of the natural food of *Nautilus* are poorly known, crop contents and remains associated with *Nautilus* in traps indicate that crabs are important in the diet. However, the variety of baits successfully used in trapping *Nautilus* in Palau and elsewhere, including shark and various bony fishes as well as chicken, dog, cat, canned sardines and the variety of food consumed by animals maintained in aquaria, indicates that *Nautilus* is neither selective nor particular in the type of food it consumes. The animal appears to be surviving as a long-lived, deep water, fore reef scavenger and sometime predator that may range widely in search of food.

Etymology. The species name *belauensis* is derived from latinization of "Belau," the traditional spelling of Palau.

Repository. The holotype of *Nautilus belauensis* (730549), paratypes (730546, 730672, 730673, 730676) and a series of reference topotypes (730534-730551; 730632-653, 730674-730676) are deposited at the U.S. National Museum of Natural History, Washington, D.C.

ACKNOWLEDGMENTS

Study of *Nautilus* in Palau has been a product of combined efforts by many individuals during the past several years. Douglas Faulkner trapped the first live animals there in 1975, brought them to my attention, and assisted immeasurably in developing plans to work in Palau. The base of operations during the summers of 1977, 1978 and 1979 was the Micronesian Mariculture Demonstration Center, where invaluable assistance was provided freely by J. P. McVey, W. M. Hamner, Marhence Madranchar, Noah Idechong, Tangadik Melimarang, Becky Madraisu,

Explanation of Figures 10 to 14

Nautilus belauensis spec. nov., Palau, West Caroline Islands

Figure 10: Animal swimming toward deep water, in typical rapid descent posture off Mutremdiu Point, Palau $\times \frac{1}{2}$

Figure 11: Live mature animal photographed in shallow water, showing relation of ocular sinus to eye; note pre-ocular and post-ocular tentacles $\times 1$

Figure 12: Freshly caught mature and immature animals. Note differences in color band distribution $\times \frac{1}{2}$

Figure 13: Apertural view of live immature animal, with protected buccal mass (center) and jaws opened, showing radula approximately $\times 1\frac{1}{2}$

Figure 14: Live mature male with exposed buccal mass and opened jaws. Note offset buccal mass, characteristic of mature males

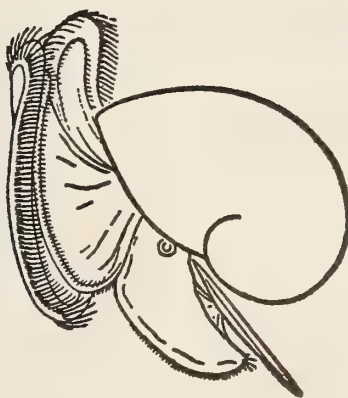
approximately $\times \frac{1}{2}$



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The Species of Living *Nautilus* and Their Distribution

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(2 Plates; 1 Text figure)

INTRODUCTION

ALTHOUGH SHELLS OF *Nautilus* have graced collectors' cabinets for centuries, until recently, relatively little has been known of the living animal. A total of 11 species and 3 variants have been named (Table 1), based for the most part upon slight variations in shell morphology and shell coloration. It is notable that all but one of these taxa (*N. belauensis* Saunders, 1981) were originally based upon isolated shells and that the soft parts of only three others (*N. pompilius* Linnaeus, 1758; *N. macromphalus* Sowerby,

1849; *N. scrobiculatus* (Lightfoot, 1786), have subsequently become known; these appear to be the only species that may be unequivocally distinguished. In spite of this, as many as six species are currently recognized by some authors (TORIYAMA *et al.*, 1965; JECOLN, 1980). A detailed systematic evaluation of *Nautilus* taxonomy will not be attempted here. However, new information on morphologic variation within individual populations and their geographic distribution provides a basis for re-evaluating the status of the various species that have been assigned to *Nautilus*. Definitive resolution of the taxonomy will require new data concerning live animals. Such information is just beginning to become available; investigations of living *Nautilus* have been conducted in the Philippines, Palau and Fiji, and large numbers of *N. macromphalus* have been studied in New Caledonia. As this study shows, there is considerable variation within individual populations of *Nautilus* and there are taxonomically significant morphological differences between geographically isolated populations, that in the past have been regarded as conspecific. Detailed study of other populations of *Nautilus* will likely reveal similar differences and will be prerequisite to final clarification of the taxonomy of this relict genus.

Table 1

Status of described *Nautilus* species
and their reported occurrences.

Species composition	Status	Reported occurrence
<i>Nautilus pompilius</i> Linnaeus, 1758	valid	Philippines to Australia
<i>N. ambiguus</i> Sowerby, 1849	nom. dub.	unknown
<i>N. stenomphalus</i> Sowerby, 1849	subsp.?	N. Australia
<i>N. repertus</i> Iredale, 1944	subsp.?	S. and W. Australia
<i>N. alumnus</i> Iredale, 1944	nom. dub.	N. Australia
<i>N. pompilius</i> var. <i>perforatus</i> Willey, 1896	syn.	New Guinea
<i>N. pompilius</i> var. <i>marginalis</i> Willey, 1896	syn.	New Guinea
<i>N. pompilius</i> var. <i>moretoni</i> Willey, 1896	syn.	New Guinea
<i>Nautilus macromphalus</i> Sowerby, 1849	valid	New Caledonia, Loyalty Islands
<i>Nautilus scrobiculatus</i> [Lightfoot, 1786]	valid	Solomons, New Guinea
<i>N. umbilicatus</i> Lister, 1685	syn.	unknown
<i>N. perforatus</i> Conrad, 1849	syn.	unknown
<i>N. texturatus</i> Gould, 1857	syn.	unknown
<i>Nautilus belauensis</i> Saunders, 1981	valid	Palau, W. Caroline Is.

CEPHALOPODA Cuvier, 1798

ECTOCOCHLIA Schwartz, 1894

NAUTILOIDEA Hyatt in Zittel, 1900

NAUTILIDAE de Blainville, 1825

Nautilus Linnaeus, 1758*Nautilus pompilius* Linnaeus, 1758

(Figures 2, 3, 6, 12)

The type species of *Nautilus*, also the most common form, is distinguished by the relatively small umbilicus

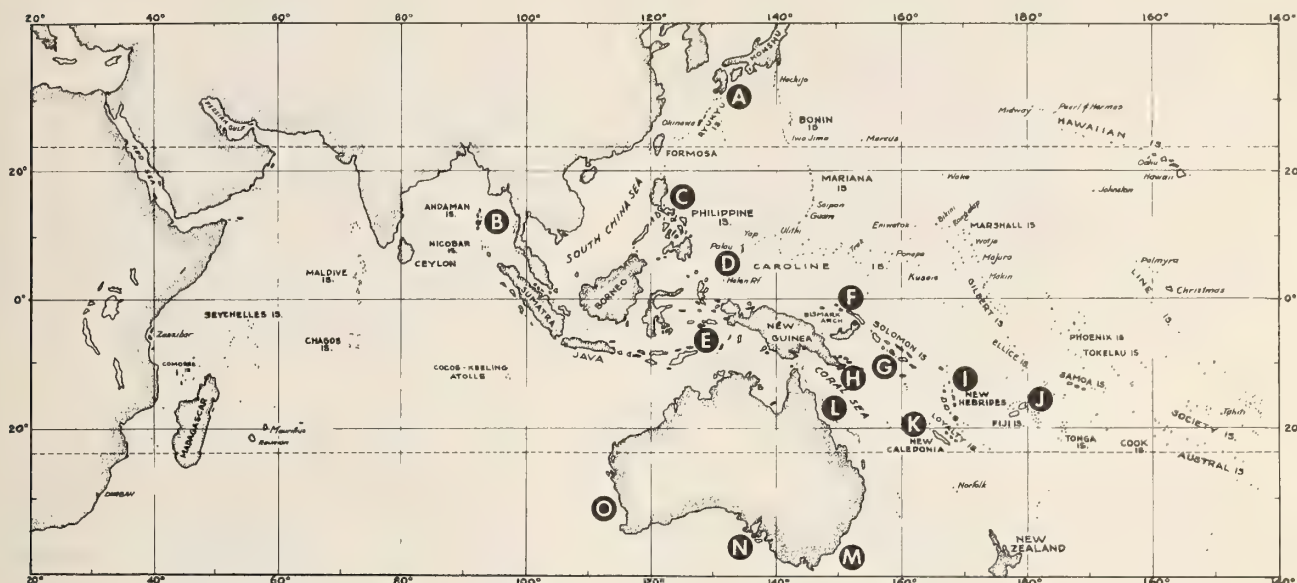


Figure 1

Documented occurrences of living *Nautilus*, based upon descriptions of living animals and reports of animals with intact soft parts, with exception of North Australia (L) from whence only shells have been reported.

A. *Nautilus pompilius*, Japan. A single live specimen was recovered at the surface, off Kawajiri, near Kagoshima Bay, southern Kyushu, Japan, April 5, 1978 (TANABE & HAMADA, 1978; HAMADA *et al.*, 1980). This and the more than 40 known occurrences of empty shells in the Japanese Islands are interpreted as drift occurrences originating from the south, on the Kuroshio current.

B. *Nautilus pompilius*, Andaman Islands. A live specimen was taken in shallow water at Port Blair, Andaman Is., and its behavior was described by SMITH (1887; reprinted in FOORD, 1888). There are numerous reports of drifted shells of *N. pompilius* in this area, including the coast of Thailand (HAMADA, 1964; TORIYAMA *et al.*, 1965), Bangladesh (TEICHERT, 1970), but Smith's report is the sole documentation of a living specimen.

C. *Nautilus pompilius*, Philippines. Shells are available from most parts of the Philippines (TALAVERA & FAUSTINO, 1931), but the best documented occurrences of living animals are from the Cebu and Negros Islands area (GRIFFIN, 1900; DEAN, 1901; HAVEN, 1972, 1977; KANIE & TANABE, 1979).

D. *Nautilus belauensis*, Palau, W. Caroline Islands. Living animals were first trapped in Palau in 1975 by D. Faulkner (DUGDALE & FAULKNER, 1976) and have subsequently been investigated by SAUNDERS *et al.*, 1978; SAUNDERS & SPINOSA, 1978, 1979; SAUNDERS, 1981.

E. *Nautilus pompilius*, Ambon (Amboina), Indonesia. The first published figures of *Nautilus* soft parts (RUMPHIUS, 1741) were from Amboina, the type locality for the species. A century and a half later, 6 live specimens were reported caught there on a hand-line by SIMON (1896) and their anatomy was described by HALLER (1895).

F. *Nautilus pompilius*, New Britain, Bismarck Archipelago. Arthur Willey trapped several hundred *Nautilus* and obtained unfertilized eggs in Blanche Bay and Talili Bay along the Gazelle Peninsula, near Rabaul (WILLEY, 1902: fig. 2).

G. *Nautilus pompilius*, Solomon Islands. Although no living specimens have been described from the Solomon Islands, drifted shells are relatively common in the area (*e.g.*, STENZEL, 1957), and 8 live animals were trapped at approximately 250 m depth in the Russell Islands by Douglas Faulkner in 1977 (personal communication).

H. *Nautilus scrobiculatus*, New Guinea. Living representatives of this species have never been documented, but a single, mutilated specimen was obtained from the surface in Milne Bay, New Guinea (WILLEY, 1899, 1902). Drifted shells are not uncommon from the New Guinea and the Solomons regions.

I. *Nautilus pompilius*, New Hebrides. The first specimen of *Nautilus* to be studied scientifically, by Sir Richard OWEN (1832), was taken at the surface in Dillon Bay, Erromanga, New Hebrides, in 1829 by George BENNETT (1834), who reported that it was used as a source of food by the natives there (1859: 227).

J. *Nautilus pompilius*, Fiji. A live *Nautilus* was recovered during the Challenger expedition, dredging off Matuku Island at a depth of 320 fathoms (ca. 192 m) (HOYLE, 1886; MOSELY, 1892). Additional reports of *Nautilus* in this region include WARD *et al.*, 1977; WARD & MARTIN, 1978, 1980; WARD, 1979.

K. *Nautilus macromphalus*, New Caledonia and Loyalty Islands. The only occurrence of *N. macromphalus* is in New Caledonia and the nearby Loyalty Islands, where the species has been well documented by WILLEY (1902); BIDDER (1962); DENTON & GILPIN-BROWN (1966); MARTIN *et al.*, (1978); and WARD & MARTIN (1980). The report of a live *Nautilus* identified as *N. stenomphalus* caught near Mare Island, Loyalty Group in 1939 (ANDERSON, 1940) is shown by illustrations to be *N. macromphalus*.

L. *Nautilus pompilius*, or *N. pompilius* (?) *stenomphalus*, or both, Queensland, N. Australia. It appears certain that living *Nautilus* occur along the Great Barrier Reef, Queensland, Australia. Although no live specimens have been documented, shells occur there commonly (IREDALE, 1944; STENZEL, 1957).

M. *Nautilus pompilius*, New South Wales, east and southeast Australia. As in the case of the N. Australian *Nautilus*, numerous occurrences of drift shells from New South Wales, eastern and southeastern Australia have been reported (IREDALE, 1944; STENZEL, 1957), but there is only one indirect report of a living specimen from Iluka, NSW (fide H. K. DUGDALE, 1975).

N. *Nautilus pompilius* (?) *repertus*, S. Australia. In 1911, a beach stranded specimen of *N. pompilius* with intact soft parts was collected in Foul Bay, southern Yorke Peninsula, and was described

by A. R. RIDDLE in 1920. This specimen was identified as *N. repertus* and figured by COTTON (1957a; 1957b: plt. 6).

O. *Nautilus pompilius* (?) *repertus*, W. Australia. The origin of the type specimens of *N. repertus*, both empty shells, was Pelsart Island, Abrolhos Group, and Rottnest Island, West Australia. Additional occurrences of drifted shells along the coast of Western Australia range from Denmark (35° S Lat.) north to Cardabia, just north of Point Maud, and Ningaloo, just north of Point Cloates (23° S Lat; Teichert, 1980, personal communication, and fide H. K. DUGDALE, 1975) where a shell with the decaying animal inside was reportedly found in 1967 (fide H. K. DUGDALE, 1979). Recently, an additional specimen was reported to have been taken alive, 225 km NNW of Port Hedland, and is in the Western Australian Museum (S. M. Slack-Smith, personal communication to T. Whitehead, 1980).

(umbilical diameter is approximately 5% of the shell diameter), which is covered by a calcareous deposit, the umbilical callus, secreted during the second whorl, or when the shell is approximately 75 mm diameter. Shell coloration is variable in both pattern and hue, but generally consists of irregularly bifurcating brown to reddish-brown stripes that extend from near the umbilicus to the venter. The body chamber of mature individuals lacks coloration and the last ventral color band often marks the approximate location of the last septum secreted. Mature Philippine specimens average approximately 170 mm diameter, with total weight (body plus shell in air) approximately 850 g (Table 2).

Distribution. *Nautilus pompilius* is the most widely distributed species (Figure 1) and living animals have been described from the Philippines (DEAN, 1901; HAVEN, 1972; 1977; KANIE & TANABE, 1979); Fiji (MOSELY, 1892; DAVIS & MOHORTER, 1973; WARD *et al.*, 1977); and a single live animal was found off Kagoshima Bay, south Japan (TANABE & HAMADA, 1978; HAMADA *et al.*, 1980). In his description of *N. pompilius*, Linnaeus stated only

that it "Inhabits the Indian and African Ocean;" (TURTON, 1806: 305). However, since his first cited reference to an illustration of both the genus and the species was that of RUMPHIUS (1741: plt. 17, figs. A-C), Amboina, the source of the specimens illustrated in Rumphius, would be the type locality.

More biological studies have been based on *Nautilus pompilius* than any other species of *Nautilus*. Excellent anatomical descriptions were published by OWEN (1832), GRIFFIN (1900) and WILLEY (1902) and others and general observations were made by DEAN (1901). Information on general ecology, biology, distribution, aquarium observations, color polymorphism, swimming, the jaw apparatus, long term movement, cameral liquid and depth distribution and implosion of living animals were described respectively by HAVEN, 1972; WARD *et al.*, 1977; BIDDER, 1962; SAUNDERS *et al.*, 1978; COLLINS *et al.*, 1980; WARD & MARTIN, 1980; KANIE *et al.*, 1980; and JECOLN, 1980. In 1978, the results of on-site physiological investigations of *Nautilus pompilius* in the Philippines were published, which yielded new information on *Nautilus* spermiogenesis, respiration, eye, muscular metabolism and hemo-

Explanation of Figures 2 to 7

Species of living *Nautilus*. All figures $\frac{1}{2}$ natural size

Figure 2: *Nautilus pompilius* Linnaeus, 1758 (DMNH 19940), Lizard Island, Queensland, N. Australia. Note lack of umbilical callus and color bands extending to umbilicus.

Figure 3: *Nautilus pompilius* Linnaeus, 1758 (DMNH 19939), N. Queensland, N. Australia. Note presence of umbilical callus and color bands extending to umbilicus.

Figure 4: *Nautilus pompilius* (?) *stenomphalus* Sowerby, 1849 (DMNH 19939), N. Queensland, N. Australia. Note lack of umbilical callus and absence of adumbilical color bands.

Figure 5: *Nautilus scrobiculatus* [Lightfoot, 1786] (DMNH 52576), Florida Island, Solomon Islands.

Figure 6: *Nautilus pompilius* Linnaeus, 1758 (USNM 730671), Tañon Straits, off Cebu, Philippines. Animal no. AH 477, caught alive 1979 Alpha Helix Expedition, mature male, trapped Nov. 8, 1979.

Figure 7: *Nautilus macromphalus* Sowerby, 1849 (DMNH 19937), New Caledonia.



Table 2

Dimensions, maturity, sex, umbilical coloration and closure in selected specimens of *Nautilus*.

Species		Spec. no.	Locality	D	U	Wm.	Wt.	Mat.	Sex	Misc.
<i>N. scrobiculatus</i>	[Lightfoot, 1786]	USNM 61395B	Indo-Pacific	190*	35	94.5		IBM	—	
<i>N. scrobiculatus</i>	[Lightfoot, 1786]	USNM 61395A	no data	179.6	38.5	84.8		M	—	
<i>N. scrobiculatus</i>	[Lightfoot, 1786]	USNM 61395A	Indo-Pacific	184	37.5	90		M	—	
<i>N. scrobiculatus</i>	[Lightfoot, 1786]	BMC 1	Honiara, Solomons	165.5*	35*	89.7		IBM	—	
<i>N. scrobiculatus</i>	[Lightfoot, 1786]	BMC 2	Honiara, Solomons	193*	41	97.3		M	—	
<i>N. scrobiculatus</i>	[Lightfoot, 1786]	BMC 3	Rabaul, Solomons	117*	27	66.5		I	—	
<i>N. scrobiculatus</i>	[Lightfoot, 1786]	DMNH 52576	Florida I., Solomons	182.3	34.5	89.7		M	—	
<i>N. scrobiculatus</i>	[Lightfoot, 1786]	DMNH 19941	Papua, New Guinea	59.2	16.5*	32.6		I	—	
<i>N. scrobiculatus</i>	[Lightfoot, 1786]	DMNH —	no data	187.3	34.6	93.0		M	—	
<i>N. macromphalus</i>	Sowerby, 1849	USNM 149909	New Caledonia	156.5	25*	77.4		IBM	—	
<i>N. macromphalus</i>	Sowerby, 1849	USNM 149909	New Caledonia	145.5	23.5*	72.4		IBM	—	
<i>N. macromphalus</i>	Sowerby, 1849	USNM 538614	New Caledonia	162.7	29*	81.7		M	—	
<i>N. macromphalus</i>	Sowerby, 1849	USNM 538614	New Caledonia	164	27*	78.7		M	—	
<i>N. macromphalus</i>	Sowerby, 1849	BMC 4	New Caledonia	123.5	26*	—		I	—	
<i>N. macromphalus</i>	Sowerby, 1849	DMNH 19937	New Caledonia	159.1	24*	78.5		M	—	
<i>N. pompilius stenomphalus</i>	Sowerby, 1849	DMNH 19939	N. Queensland	144.3	8.5*	72.8		M	—	white adumbilicus
<i>N. pompilius stenomphalus</i>	Sowerby, 1849	DMNH 19940	Lizard I., Queensland	139.4	7.0*	66.0		M	—	striped umbilicus
<i>N. pompilius</i>	Linnaeus, 1758	DMNH 19939	N. Queensland	131.5	—	65.0		MB	—	striped umbilicus
<i>N. pompilius</i>	Linnaeus, 1758	AH 614	Tañon Straits, Philippines	73.5	—	39.0	69	I	F	umbilicus closing
<i>N. pompilius</i>	Linnaeus, 1758	BMC 5	Philippines	62*	5*	33		I	—	umbilicus open
<i>N. pompilius</i>	Linnaeus, 1758	BMC 6	Philippines	61*	5	33		I	—	umbilicus half-closed
<i>N. pompilius</i>	Linnaeus, 1758	BMC 7	Philippines	75	8	40		I	—	umbilicus closed
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 319	Tañon Straits, Philippines	177	—	87.3	925	M	M	
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 353	Tañon Straits, Philippines	168.5	—	80.3	762	IBM	F	
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 383	Tañon Straits, Philippines	170.3	—	84.2	864	M	M	
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 404	Tañon Straits, Philippines	171.2	—	81.4	764	M	F	
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 420	Tañon Straits, Philippines	175.9	—	86.4	945	M	M	
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 421	Tañon Straits, Philippines	168.9	—	82.9	810	M	F	
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 424	Tañon Straits, Philippines	171.2	—	86.3	904	F	M	
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 433	Tañon Straits, Philippines	150.2	—	72	574	M	F	
<i>N. pompilius</i>	Linnaeus, 1758	USNM 730671	Tañon Straits, Philippines	186.4	—	91.6	1055	M	M	
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 491	Tañon Straits, Philippines	173.5	—	84.7	861	M	M	
<i>N. pompilius</i>	Linnaeus, 1758	BMC-AH 575	Tañon Straits, Philippines	173.7	—	85.8	868	M	M	
<i>N. belauensis</i>	Saunders, 1981	BMC 866	Palau, W. Caroline Is.	85	6*	43.5	111	I	—	umbilicus open
<i>N. belauensis</i>	Saunders, 1981	USNM 730672	Palau, W. Caroline Is.	101.7	7*	52.4	170	I	—	umbilicus open
<i>N. belauensis</i>	Saunders, 1981	BMC 914	Palau, W. Caroline Is.	110.3	—	59.4	—	I	—	umbilicus closed
<i>N. belauensis</i>	Saunders, 1981	USNM 730673	Palau, W. Caroline Is.	211.4	9*	96.5	1462	IBM	M	umbilicus open
<i>N. belauensis</i>	Saunders, 1981	BMC 257	Palau, W. Caroline Is.	212.2	8.1*	103.4	1590	IBM	M	umbilicus open
<i>N. belauensis</i>	Saunders, 1981	BMC 37a	Palau, W. Caroline Is.	214	11*	99	1098	M	M	umbilicus open
<i>N. belauensis</i>	Saunders, 1981	USNM 730549	Palau, W. Caroline Is.	216	—	103.5	1449	M	M	
<i>N. belauensis</i>	Saunders, 1981	USNM 730674	Palau, W. Caroline Is.	149.7	—	72.4	455	I	F	
<i>N. belauensis</i>	Saunders, 1981	USNM 730534	Palau, W. Caroline Is.	218.8	—	101.7	1543	M	M	
<i>N. belauensis</i>	Saunders, 1981	USNM 730535	Palau, W. Caroline Is.	208.8	—	100	1421	I	M	
<i>N. belauensis</i>	Saunders, 1981	USNM 730536	Palau, W. Caroline Is.	209.5	—	99.8	1443	M	M	
<i>N. belauensis</i>	Saunders, 1981	USNM 730537	Palau, W. Caroline Is.	198.2	—	87.2	—	M	F	
<i>N. belauensis</i>	Saunders, 1981	USNM 730675	Palau, W. Caroline Is.	215.8	—	106.4	—	M	M	white adumbilicus
<i>N. belauensis</i>	Saunders, 1981	USNM 730676	Palau, W. Caroline Is.	190	—	85.1	—	M	F	
<i>N. belauensis</i>	Saunders, 1981	USNM 730546	Palau, W. Caroline Is.	205.3	—	95.5	1238	IBM	F	

D, maximum shell diameter; U, umbilical diameter measured across umbilical shoulders; Wm, maximum width at aperture (all measurements in millimeters); Wt, weight (gms) of body plus shell in air at time of capture; Mat, animal maturity, classed as: M, fully mature, displays all mature characteristics including blackened and thickened aperture, deepened ocular, hyponomic sinuses, white

body chamber; MB, barely mature, with aperture barely blackened and thickened; IBM, submature, without apertural blackening or thickening, but with full size, white body chamber; I, immature, shows no characteristics of maturity (for details see Saunders and Spinoso, 1978). Sex determined by sexing of live animals. Asterisked measurements are approximate.

dynamics (ARNOLD; ARNOLD & ARNOLD-WILLIAMS; JOHANSEN *et al.*; HURLEY *et al.*; REDMOND *et al.*; HOCHACHKA *et al.*; BOURNE *et al.*; all 1978).

Nautilus belauensis Saunders, 1981

(Figures 8-11)

This recently named species of *Nautilus* has the same basic shell form as *N. pompilius*, but is distinguished by a) its larger mature size (mature shell diameter approx. 200 mm; body plus shell weight approx. 1300 g), with relatively late umbilical closure (*ca.* 110 mm diameter) in contrast to *N. pompilius* (see previous description); b) the presence of fine, longitudinally crenulated growth lines, producing a concentrically lirate texture (Figures 8, 10, 11); c) broadly triangular central rachidian and second lateral radular teeth (for details see SAUNDERS, 1981). Coloration of the shell is the same as in *N. pompilius* and exhibits similar variation in patterns (see Discussion).

Distribution. *Nautilus belauensis* is presently known only from Palau, W. Caroline Islands, with the exception of a single empty shell found in Mindanao, Philippines, that had been tagged and released alive in Palau (Figure 8). Various aspects of the Palauan form have been described by SAUNDERS *et al.* (1978), SAUNDERS & SPINOSA (1978, 1979) and SAUNDERS (1981).

Nautilus macromphalus Sowerby, 1849

(Figure 7)

This species is similar to *Nautilus pompilius* in size and coloration but is distinguished by its prominent, open umbilicus with inwardly sloping umbilical walls and the evenly rounded umbilical shoulder. The umbilical diameter (U/D) in mature shells is approximately 16% shell diameter; mature shell size is approximately 160 mm diameter.

Distribution. *Nautilus macromphalus* is known only from New Caledonia and the adjacent Loyalty Islands, where the living animal was first studied by Arthur WILLEY (1902) and later by BIDDER (1962), DENTON & GILPIN-BROWN (1966), WARD & MARTIN (1978, 1980) and WARD (1979); aquarium-based studies of this species have been published by HAMADA & MIKAMI (1977), MIKAMI & OKUTANI (1977), and by the Japanese Expert Consultation on Living Nautilus (JECOLN, 1980).

Nautilus scrobiculatus (Lightfoot, 1786)

(Figure 5)

The rarest and perhaps most distinctive species of *Nautilus* is *N. scrobiculatus*. It is distinguished by a large umbilicus (U/D approximately 20%) that exhibits subangular umbilical shoulders and vertical walls. The shell coloration consists of narrow bands, that may not extend to the umbilicus and that tend to coalesce across the venter. As in *N. belauensis*, the shell surface of this species is distinctly reticulate or scrobiculate, as a result of irregularly crenulate longitudinal lirae intersecting the radial growth lines. Mature shell size is approximately 180 mm diameter. Synonyms that were based on variants of *N. scrobiculatus* include *N. umbilicatus* Lamarck, 1822; *N. perforatus* Conrad, 1849; and *N. texturatus* Gould, 1857.

Distribution. *Nautilus scrobiculatus* is a rare species, and a live specimen has never been reported. Willey did obtain "a single mutilated specimen . . . accompanied by its shell, which had been picked up from the surface of the sea, not far from Milne Bay in British New Guinea . . ." and he noted that this species "differed noticeably from its congeners by the character of the hood, the gibbositities of which have the form of flat-topped angular areas separated by deep grooves, producing a pronounced tessellated appearance" (WILLEY, 1902: 744; pl. 78, fig. 3). The origin of most shells, presumably all drifted specimens, appears to be New Guinea and the Solomon Islands.

QUESTIONABLE SPECIES

Nautilus stenomphalus Sowerby, 1849

(? Figure 4)

Little information is available concerning this form of *Nautilus* and its validity must be regarded as questionable. SOWERBY (1849: 465) described the species as "nearly similar in shape to *N. macromphalus*, but distinguished by the smallness of its umbilicus, the subinternal margin of which is slightly angular: in colouring it is like *N. ambiguus*." In point of fact, the shell form of *N. stenomphalus* is identical to that of *N. pompilius*, except that the umbilicus lacks a callus, and remains open at maturity. The color bands on the specimen figured by Sowerby (*op. cit.*: pl. 97, fig. 3) are restricted to the venter and ventrolateral region, leaving a white adumbilical area, as in his *N.*

ambiguus. It may be that *N. stenomphalus* is a variant that occurs with normal, callus-bearing *N. pompilius* such as described by IREDALE (1944) as *N. alumnus* (see below). This interpretation is supported by three specimens from N. Queensland, Australia, in collections at the Delaware Museum of Natural History, Greenville, Delaware (Figures 2-4). One (DMNH 19939; Figure 4) closely matches Sowerby's definition of *N. stenomphalus*, in lacking both umbilical callus and adumbilical color bands; however, the second specimen (DMNH 19940; Figure 2), which also lacks an umbilical callus, has color bands extending to the umbilicus; the third (DMNH 19939; Figure 3) has an umbilical callus and color bands extending to the umbilicus. These three specimens thus span the conceptual definitions of three species: *N. stenomphalus*, *N. ambiguus* and *N. pompilius*; clearly, investigation of the N. Australian form will shed more light upon variation within an individual population of *Nautilus*.

Distribution. No locality for *N. stenomphalus* was cited by SOWERBY (1849), but as discussed above, shells have been reported from North Queensland, Australia (IREDALE, 1944).

Nautilus alumnus Iredale, 1944

This species was proposed for *Nautilus* from North Queensland "not exceeding 6 inches in diameter ..." with "... only some twelve to fourteen (color bands ...)" (IREDALE, 1944: 295). The range of variation in the color patterns of *Nautilus* makes this distinction alone inadequate, and since no specimen was figured, *N. alumnus* is regarded as a *nomen dubium*.

Nautilus ambiguus Sowerby, 1849

In describing this species, SOWERBY stated (1849: 464, 465), that it might be a sexual variant of *N. pompilius*, but that it was distinguished by a wider aperture and by the reduced color pattern, which lacks color stripes extending to the closed umbilicus. However, the *ambiguus*-like color pattern occurs as a variant in populations of *N. pompilius* and *N. belauensis* (see Discussion), and used alone would be an inadequate criterion for species recognition. Sowerby's statement that this species might be a sexual variant is probably correct with respect to the broader aperture, for this characterizes mature males (SAUNDERS & SPINOSA, 1978). Additionally, the size of the specimen illustrated by SOWERBY (1849: pl. 97, fig. 2) was not

indicated. Since all of the characters cited by Sowerby refer to variations, *N. ambiguus* should be regarded as a *nomen dubium*.

Distribution. SOWERBY (1849) did not cite the origin of the specimen that he illustrated; however shells with a similar color pattern occur among typically colored shells of *N. pompilius* in the Philippines, Fiji and N. Australia.

Nautilus repertus Iredale, 1944

The original description of *Nautilus repertus* by Iredale (1944) was minimal; it was based upon a single shell and a drawing of another from Western Australia. The species was said to be distinguished by its large size (216-228 mm diameter) and by the lack of color bands in the umbilical region. This color pattern is the same as that said to characterize *N. ambiguus*. However, the combination of the reduced color pattern and the large mature size do appear to be consistent in characterizing this southern and western Australian form, although very limited numbers of shells are available.

Distribution. The two shells described by Iredale (1944) were found at Pelsart Island, Houtmans Abrolhos, and Rottnest Island, Western Australia. The find of a *Nautilus* with soft parts intact in Foul Bay, Yorketown, southern Yorke Peninsula, South Australia, was described by RIDDLE (1920). This specimen was subsequently figured by COTTON (1957a, b) and identified as *N. repertus* on the basis of its large shell size (228 mm diameter) and similar color pattern.

Nautilus moretoni Willey, 1896

In the course of his three-year study of *Nautilus* (1895-1897) in the southwest Pacific, Arthur Willey examined hundreds of live-caught specimens of *N. pompilius* and *N. macromphalus*. He paid particular attention to variation in *N. pompilius* and named a series of variants, including *N. pompilius* var. *perforatus*, var. *marginalis* and var. *moretoni*, based upon the degree of development of the umbilical callus (WILLEY, 1896). One of Willey's variants, *N. moretoni*, was subsequently elevated to species rank by SHIMANSKY & ZHURAVLEVA (1961; see MAPES *et al.*, 1949). However, this character is both highly variable and non-systematic in individual populations of *N. pompilius* (see Discussion), and should not be accorded systematic significance.

DISCUSSION

The three species *Nautilus pompilius*, *N. macromphalus* and *N. scrobiculatus* differ in overall form to the extent that no question has been raised regarding their distinction or validity. The identity of the recently named species *N. belauensis* is well established on the basis of distinction in both hard and soft parts observed in more than 100 live specimens. By contrast, the questionable species *N. stenomphalus*, *N. alumnus*, *N. ambiguus*, *N. repertus* and *N. moretoni* were distinguished on the basis of features that may be highly variable within individual populations, including color pattern, umbilical closure and mature shell size. For example, the umbilical callus may be developed to varying degrees or may even be absent altogether. Of more than 100 *Nautilus belauensis* trapped alive and examined during the course of studies in Palau, W. Caroline Islands (SAUNDERS & SPINOSA, 1978, 1979), the shells of four animals lacked an umbilical callus altogether at maturity (Figures 9, 10), and in several others a callus had been deposited on only one side of the shell. Similarly, the lack of adumbilical color bands, which has been used to distinguish three separate *pompilius*-like species (*N. repertus*, *N. ambiguus* and *N. stenomphalus*), occurs as a variant in Philippines, Palau, and Fiji *Nautilus* populations (Figure 11; see also WARD *et al.*, 1977). Mature shell size can also vary considerably. Thirteen mature *N. pompilius* from Fiji (WARD *et al.*, 1977; COLLINS *et al.*, 1980) ranged from 137-152 mm maximum diameter (mean 145 mm); mature specimens from the Philippines obtained by the 1979 Alpha Helix expedition ranged from 150-188 mm (mean 170 mm) and the size range of 375 mature *N. belauensis* described by SAUNDERS & SPINOSA (1978) was 180-230 mm (mean 204 mm).

Clearly, the range of variation within individual populations of *Nautilus* may span the various combinations of characters that past authors have used to distinguish species. Each of the features cited as distinguishing *N.*

ambiguus (lack of adumbilical color bands), *N. stenomphalus* (lack of an umbilical callus) and *N. repertus* (large size, lack of adumbilical color bands) may occur within a single population of *N. pompilius*. However, recent investigations of large numbers of living animals have also made it apparent that there are consistent differences between isolated populations of *Nautilus* that previously have been regarded as belonging to the same species. As cited above, size alone distinguishes some geographically isolated *Nautilus pompilius* (e.g., Fiji vs. Philippines populations) and specific color patterns (e.g., lack of adumbilical bands, as in *N. repertus* from W. and S. Australia) or the lack of an umbilical callus (as in *N. stenomphalus* from N. Australia) may prove to characterize other populations. Such differences would not be unexpected among such geographically isolated forms, but whether they constitute discrete species remains questionable. It might be preferable to regard such geographically isolated forms, distinguished by features that occur as variants in other populations, as subspecies. Using this approach, 4 discrete species, *N. pompilius*, *N. macromphalus*, *N. scrobiculatus*, and *N. belauensis* are recognizable; the forms described as *N. stenomphalus* and *N. repertus* would be regarded as questionable subspecies of *N. pompilius*, pending additional information on the morphology of living animals and the variation within populations (particularly among the poorly known Australian forms).

Distribution of *Nautilus*. Considering the generally deep, remote habitat of living *Nautilus* and the high potential for postmortem drift of the buoyant shell, it is not surprising that present knowledge of the geographic distribution of *Nautilus* and its component species must be regarded as tenuous. Documented occurrences of living animals, or of shells with intact soft parts, are limited to just 14 discrete regions within the Indo-Pacific (Figure 1). These range from the northernmost occurrence, off southern Japan, to southern Australia, and from the Andaman

Explanation of Figures 8 to 12

Variation in *Nautilus*

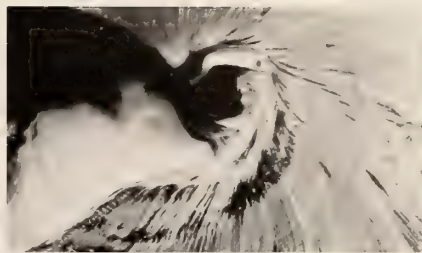
Specimens of *Nautilus belauensis* Saunders, 1981, trapped off Mutremdiu Point, Palau, W Caroline Islands (Figures 8-11) and drift shell of *Nautilus pompilius* from Majuro, Marshall Islands (Figure 12). All figures $\frac{1}{2}$ natural size except Figure 5 ($\times 1.7$). Figure 8: *Nautilus belauensis* Saunders, 1981 (BMC 0532), mature male tagged and released alive in Palau, January 27, 1978; shell recovered June 14, 1978 by J. Maranan and F. Malaki at Jose Abad Santos, Mindanao, Philippines (see SAUNDERS & SPINOSA, 1979).

Figures 9, 10: *Nautilus belauensis* Saunders, 1981 (Paratype, US NM 730673), submature male, lacking umbilical callus. Encrusting serpulids, such as shown here in umbilicus, are common on living animals.

Figure 11: *Nautilus belauensis* Saunders, 1981 (Topotype, USNM 730675), mature male, lacking adumbilical color bands on shell. Figure 12: *Nautilus pompilius* Linnaeus, 1758 (DMNH 42210), beach stranded shell, Majuro.



8



9



10



11



12

Islands in the west, eastward to the Fiji Islands, spanning an area of approximately 8 000 by 9 000 km. By contrast, the occurrence of the drifted shells of *Nautilus* is considerably greater, ranging from the east coast of Africa, eastward to Samoa and the Tonga Islands and from Japan to as far south as New Zealand (see HAMADA, 1964; STENZEL, 1964; TORIYAMA *et al.*, 1965; TEICHERT, 1970; HOUSE, 1973; JECOLN, 1980). It is rarely possible to determine the actual geographic origin of drifted shells, although drift of 1000 km in 138 days, from Palau to Mindanao, has recently been documented (Figure 8; see also SAUNDERS & SPINOSA, 1979). In addition, it may not be possible to distinguish shells representing endemic occurrences from distantly transported drift specimens. For example, the occasional shells of *N. belauensis* found on the beaches of Palau were regarded as drifted specimens, until live animals were actually trapped there in 1975. It is reasonable to predict that some, perhaps many, of the drift occurrences reported in the literature will be found to reflect the occurrences of living endemic populations. For example, the presence of fresh drift shells of *N. pompilius* in Majuro, Marshall Islands (Figure 12), and off Kusaie, the easternmost of the Caroline Islands, in the Ponape district (R. Grifford, personal communication, 1977) are upcurrent from potential sources for drift shells and may well indicate the presence of living *Nautilus*. This is not intended to imply that *Nautilus* will eventually be found to be a ubiquitous component of Indo-Pacific island reefs; in fact, to the contrary, it appears that its distribution may be spotty and unpredictable.

Only limited generalizations can be made concerning the actual geographic distribution of individual species of the genus. *Nautilus pompilius* is by far the most common and widely occurring species, being known throughout the entire range of the genus, with one exception; it has not been found in the New Caledonia-Loyalty Island region, which is the only area where *N. macromphalus* occurs. Thus, these two species appear to be morphologically distinct and geographically well isolated and allopatric. *Nautilus belauensis* is presently known only from Palau. Although practically no data exist concerning the range of living *N. scrobiculatus*, it appears to be restricted to the southern New Guinea-Solomon Islands region, where *N. pompilius* is also known to occur.

While the present distribution of *Nautilus* is broad, spanning most of the Indo-Pacific, it hardly compares with the distribution of shelled cephalopods in the fossil record. As recently as the Miocene Epoch (7-26 MYA), the genera *Aturia* and *Eutrephoceras* were cosmopolitan, with numerous species that were locally abundant, even in the eastern hemisphere. *Nautilus* is clearly a relict form closely

related to *Eutrephoceras* (KUMMEL, 1956), but its history is very poorly known from the post-Miocene (Pliocene and Pleistocene) to the Recent. The cause and meaning of the present distribution is unknown at this time. It may be the product of steadily contracting range caused by an inability to respond to increasing competition from the swifter, more agile teleost fishes. This is supported by the fossil record, which shows that the rapid radiation of the teleosts began in the early Cretaceous, and is complementary to the rapid decline of the shelled cephalopods, culminating in the extinction of the ammonites at the end of the period. There is simply insufficient information concerning the geographic distribution, the status and role of *Nautilus* in its natural habitat to permit more than speculation at this time. However, the general trend of reduction in diversity and distribution of the shelled cephalopods since the Cretaceous (75 MYA), and particularly of the nautiloids since the Miocene, does not favorably portend their future. By contrast, the range of morphologic variation within individual living populations and the degree of difference between isolated populations ascribed to the same species may be regarded as an encouraging indication of sufficient remaining genetic plasticity to permit survival, and perhaps even renewed speciation, within this ancient lineage.

ACKNOWLEDGMENTS

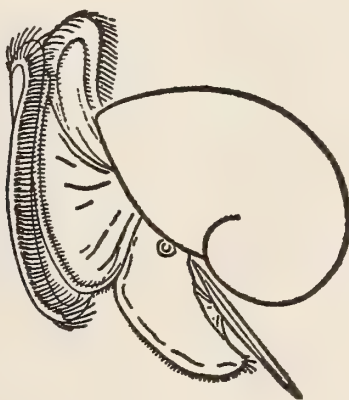
Evaluation of the species of *Nautilus* and their distribution is an outgrowth of paleobiologically oriented studies of the genus, based primarily upon *N. belauensis* in Palau, W. Caroline Islands. Information concerning the other species and their occurrence has benefitted from examination of comparative collections at the U.S. National Museum, Washington, D.C. (USNM); the Delaware Museum of Natural History, Greenville, Delaware (DMNH) and from the 1979 Alpha Helix expedition to the Republic of the Philippines, sponsored by the National Science Foundation. The assistance of R. T. Abbott, Melbourne, Florida; J. M. Arnold, University of Hawaii; R. Cichocki and R. Jensen, Delaware Museum of Natural History; H. K. Dugdale, Greenville, Delaware; M. R. House, The University of Hull, England; K. Ridgway, Colby College; C.F.E. Roper, U.S. National Museum; S. M. Slack-Smith, Western Australian Museum, Perth; C. Spinosa, Boise State University; C. Teichert, University of Rochester; G. Vostreys, Academy of Natural Sciences, Philadelphia and T. Whitehead, Chapel Hill, Queensland, Australia, during the course of this review is particularly appreciated. The location and source of indi-

vidual specimens is shown by prefix designations; BMC, collections of W. B. Saunders, Bryn Mawr College; AH, trapped during 1979 Alpha Helix expedition. My work on *Nautilus* in Palau was supported by the National Science Foundation (Grants DEB 77-14467 and EAR-8100629) and by the Committee on Research and Exploration of the National Geographic Society.

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Field Ecology and Natural History of *Cerithidea californica*

(Gastropoda: Prosobranchia)

in San Francisco Bay

BY

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(7 Text figures)

INTRODUCTION

Cerithidea californica (Haldeman, 1840), the California hornsnail, is the only native Potamidid on the California coast. It ranges from central Baja California, Mexico, to Tomales Bay, California, and typically inhabits *Salicornia* marshes, intertidal creeks, and mudflats of bays and estuaries along the coast (MACDONALD, 1967). In San Francisco Bay, however, *Cerithidea* is found primarily in marsh pans, while the introduced Atlantic mudsnail *Ilyanassa obsoleta* (SAY, 1822) occurs in tidal creeks and on mudflats.

Populations of *Cerithidea* in San Francisco Bay, formerly widespread and common throughout the Bay, are restricted now to the southern portions of the Bay. It has been suggested that the decrease of *Cerithidea* in San Francisco Bay might be related to, 1) habitat destruction through the filling of *Salicornia* salt marshes and higher intertidal mudflats, and 2) the possible influence of the Atlantic mudsnail, *Ilyanassa obsoleta* (CARLTON, 1976).

Information on the physiology and ecology of *Cerithidea californica* is limited to six studies, three of which are unpublished (MACDONALD, 1967; WHITLATCH, 1972; DRISCOLL, 1972; YOSHINO, 1975; SCOTT & CASS, 1977; McCLOY, 1979). This field study was designed to determine, 1) the life cycle, natural history, and physiological tolerances of *C. californica* in San Francisco Bay; 2) annual population fluctuations, microhabitat utilization, and activity patterns in the field; 3) growth rates from mark-recapture studies; and 4) similarities and dissimilarities between populations of *Cerithidea* in San

Francisco Bay and elsewhere. This information, collected over a four-year period, was used in conjunction with field experiments on interference competition to explain the observed displacement of *Cerithidea* from creeks and mudflats in San Francisco Bay (RACE, 1979).

SAMPLING LOCATIONS AND METHODS

Populations of *Cerithidea californica* were studied during 1975 to 1979 in the south end of San Francisco Bay (Newark, Fremont, Hayward, and Palo Alto, California) and in Bolinas Lagoon, a small estuary located about 25 km north of San Francisco Bay (Figure 1). Most quantitative data were gathered in the Fremont area at a study site shown in Figure 1. Monthly quadrat samples were taken from December, 1976 to December, 1978 during low tides at the principal study site along a predetermined transect through main creek, side creek and pan areas. Three replicate samples of numbers of live snails per quadrat were counted at each pan and creek station. An additional three replicate quadrats were counted at each pan station in the edge habitats beneath the *Salicornia* vegetation. All densities were measured with a 0.06 m² circular quadrat, counting both surface dwelling and burrowed (1-3 cm) snails greater than 10 mm. Smaller snails were not counted because their minute size and extremely high densities in late summer made them impossible to count in the field. Data from the main creek are not reported in this paper because that habitat was occupied exclusively by *Ilyanassa obsoleta* throughout the year.

Samples of adult *Cerithidea californica* (> 20 mm) for temperature tolerance experiments were collected in summer and winter from both Bolinas Lagoon (vicinity of

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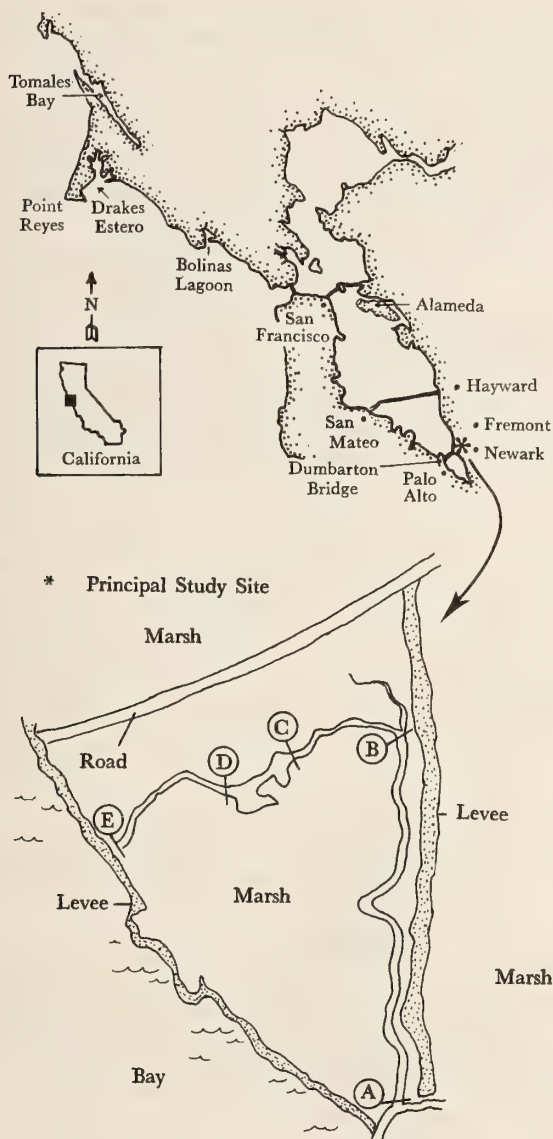


Figure 1

Map of Sampling Locations and Principal Study Site

The transect within the Principal Study Site included main creek, side creek, and pan habitats. Twelve sampling stations were in the main creek (A-B); nine in the side creek (B-C); and fifteen in pan habitats (C-E). Two types of pan habitats were distinguished on the basis of shape; main pan (C-D), a pond-like depression; and back pan (D-E), a creek-like extension of the main pan. Both pan areas were inhabited by high densities of *Cerithidea*.

Kent Island) and San Francisco Bay (vicinity of principal study site, winter, and San Mateo Bridge, summer). Prior to heat treatment, snails were kept in aerated tanks for two weeks in a 13°C cold room (winter) or in room temperature sea water (summer). For the experiment, one hundred snails each from the Bolinas and San Francisco Bay populations were placed in separate glass aquaria filled with aerated sea water at the temperature of acclimation. Both aquaria were submerged side-by-side in a large water bath (Labline Instruments Bath) with a heater mixer (Braun Thermomix II) that heated the inside bath at a rate of 1°C/5 min until the aquaria reached 40°C. Temperatures in the aquaria during the experiment were maintained at $40 \pm 1^\circ\text{C}$. At selected time intervals, a subsample of 20 snails from each aquarium was removed and placed in bowls of previously aerated sea water at room temperature. Survival of each subsample was recorded 24 hours following removal from the heated aquaria. Control snails were placed in room temperature sea water for the duration of the heat treatment experiments. Snails were recorded as alive if they were attached by the foot to the bottom or sides of the bowl. Snails were also judged alive when they were lying on the bottom with portions of the foot exposed if they quickly withdrew into the shell when poked.

In desiccation experiments, one hundred adult snails (> 20 mm) each from San Francisco Bay and Bolinas Lagoon were collected within 16 hours of each other and placed in aerated, room temperature sea water. Snails were removed from water, blotted dry, and placed in dry, paper-lined aquaria in a south-facing room with natural photoperiod. After various lengths of exposure to dry conditions at room temperature and ambient humidity, equal subsamples (15 or 20) of snails were removed from each aquarium and placed into room temperature, previously aerated sea water. Percent survival of snails for each exposure treatment was recorded after 24 hours in sea water using the same criteria for "alive" as were used in the heat treatment experiments.

Growth of *Cerithidea* was monitored throughout the year in different habitats by recording sizes of marked, recaptured snails. Snails were collected from the marsh north of the principal study site, brought to the laboratory, and kept in room temperature (summer) or 13°C (winter) aerated sea water during marking. All snails were returned to the field within one week of marking.

To prepare for marking, shells were lightly sanded by rubbing with wet-dry sand paper. Except for the first group, all snails were marked with numbered bee tags

(Chr. Grase K. G. Fabrik für Biengeräte, 7057 Endersback bei Stuttgart, Postfach 7, West Germany) attached with either Krazy Glue or Loctite Super Bonder 495 (Loctite Corp., Newington, CT). Snails in the first group were marked by embedding small numbered paper tags in a dot of epoxy on the shell (Poxy Quick, Permalite Plastics Corp., Newport Beach, CA) and covering the tags with several layers of clear nail polish. When these numbers faded over time, snails were re-identified by the unique configuration of the epoxy on the shell. All tags were affixed on the side opposite the aperture, centered on the body whorl of the shell. During a two-year period, nine groups of snails were marked and released in various habitats ranging from pans to mudflats. Of the nine groups of snails, five were caged to keep them in the appropriate habitat. Construction of the cages is described in RACE (1981).

Of the nearly 900 snails originally marked, more than 300 were recaptured on one or more occasions. In the analysis of growth, each recapture has been treated as a separate entry in the growth rate calculations. Thus, data from a snail initially 19 mm, recaptured at 21 mm, and again at 25 mm would be used to calculate two separate growth rates for snails of initial sizes 19 and 21 mm. All measurements of size (apex to bottom of aperture) were made with vernier calipers, recording length to the nearest 1/10 mm. Variation in measurement was estimated to be ± 0.1 mm. Each snail was returned to its appropriate habitat immediately following measurement.

NATURAL HISTORY AND LIFE CYCLE

1. Reproduction and Early Growth

In this species the sexes are separate (MACDONALD, 1967). Copulation between adult snails occurs during late spring and summer and is followed by the deposition of egg capsules beginning in early May. Egg capsules were present on the substrate from May to the end of September in both 1977 and 1978, occurring most densely in pan habitats, and only occasionally in creeks or mudflat areas. Size at first reproduction is about 22-24 mm as indicated by laboratory observations of adults separated by size. Growth data suggest that at this size snails are two years or older.

Egg cases of *Cerithidea californica* are elongate in form, ranging from 10-170 mm in length ($\bar{X} = 69$ mm, $n = 335$), and are composed of several rows of eggs in a mucous sheath covered with silt and fecal pellets. Individual eggs within 3 replicate lengths from 4 different egg

cases were counted, using a dissecting microscope. In 5 mm of case, the number of eggs ranged from 56 to 169 ($\bar{X} = 90$, $n = 12$). Larvae pass the veliger stage within the egg case from which they hatch and crawl away as young snails beginning some time in June. Newly hatched snails are approximately 0.25 mm and have shells composed of one or two whorls. By August, the largest individuals of the year class are approximately 2 mm with 6 whorls to the shell. In early fall, juvenile snails ranging from 0.25 mm to 3 mm are evident in the population. Figure 2 is a composite graph illustrating the early growth rate measured from the cohort that settled in summer of 1976. Mean sizes at hatching and in August have been estimated from data collected for individuals settling in summer of 1977. Measurements for these two smallest groups of snails were made in the laboratory under a dissecting microscope

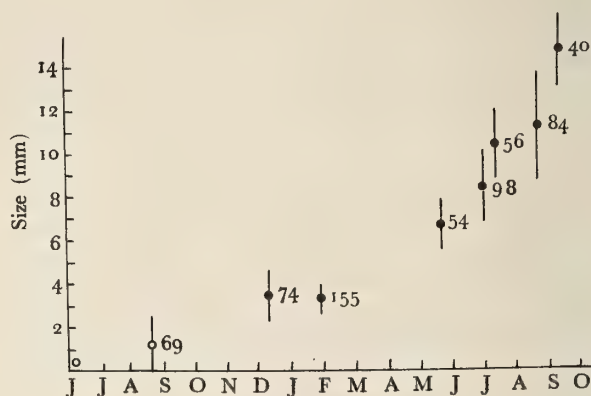


Figure 2

Growth of newly settled *Cerithidea californica* in pan habitats. Mean \pm S. D. numbers indicate sample size. Size at settlement and size in August were estimated from snails settling in Summer, 1977. All other data were from snails settling in Summer, 1976.

after separating the snails in wet sieves. The mean size of juvenile snails in August is about 1 mm. After a winter period of slow or no growth, the first year class resumes growth in the following spring, at which time individuals in the cohort range from 5 to 8 mm. By the end of their second summer, juveniles are, on the average, 15 mm.

Density of newly hatched snails was measured in the field in October 1977 with a corer of 5 cm diameter pushed into the top 1 to 2 cm of mud. Multiple core samples from two pan locations yielded mean densities equivalent to 69 000 per m² in the main pan ($n = 6$) and 200 000 per m² in the back pan ($n = 3$). Still other pan areas were

found to have no newly settled snails, indicating the patchy nature of the yearly recruitment.

2. Dispersal

After egg cases are deposited on the substrate, they stick on the mud, with the eggs developing in place. Because there is no planktonic larval form, dispersal is limited to movements of juveniles and adults.

The juvenile phase offers the best opportunity for dispersal. Juveniles (sizes 1-10 mm, and probably smaller as well) were observed during high tides hanging upside down attached by their foot to the surface film of the water and moving with the water currents. While no direct measurements of this dispersal were made in the field, the results of this floating behavior can be inferred from size frequency data in several pans.

In summer 1977, many pans lacked one-year old snails, possibly due to the drought during the previous summer which often dried pans completely between periods of tidal inundation. In early and mid-summer, the majority of snails in these pans were over 15 mm (Figure 3). At the end of the summer, following a series of very high tides, a cohort of one-year old snails appeared in the pan. It is unlikely that these juveniles crawled to this location, be-

cause the nearest pan was more than 5 m away separated by dense vegetation in which the density of snails during the summer was always near zero.

Juvenile floating behavior may also transport young snails to new habitats such as tidal creeks. Juveniles were found occasionally in tidal creeks during the summer where no egg cases or adult snails were previously seen. Because of the distance involved, it is unlikely that these young snails had arrived in these areas by crawling.

Adult snails are capable of dispersal, but only by crawling. Snails larger than about 10 mm were never observed floating on the surface film. Adult movement and dispersal is variable as indicated by mark-recapture studies. In one particular pan, marked adults remained for over two years, many never moving more than 2 m from the original point of release. The maximum movement was observed in a group of adults experimentally transplanted onto a mudflat. Many of these individuals moved as much as 10 m in just 12 hrs. In general, while adult *Cerithidea* are physically able to move long distances, it is likely that only limited dispersal activity is normally associated with this stage of life.

3. Physiological Tolerances

a. Salinity

Annual extremes of salinity for *Cerithidea* undoubtedly range from virtual freshwater in winter after heavy rains (SCOTT & CASS, 1977) to hypersaline conditions during midsummer when the water in pans disappears. Summer salinities were often above 40‰ for periods of over one month in the same pan habitat. The maximum recorded salinity was 47‰. Winter salinities were never recorded below 13‰, although no samples were taken on rainy days. *Cerithidea* can withstand extremes of inundation as well. Some populations were observed in pans that were constantly filled with water, while others were exposed to completely dry conditions for as long as several weeks between extreme high tides. Because the snails are never exposed to extreme highs of salinity in totally submerged conditions, experiments were not undertaken to test the actual upper limit of salinity for *Cerithidea*.

b. Temperature

Water temperatures in the pans varied from lows of about 5°C in winter to highs of over 30°C in summer. Actual maximum temperatures to which *Cerithidea* was

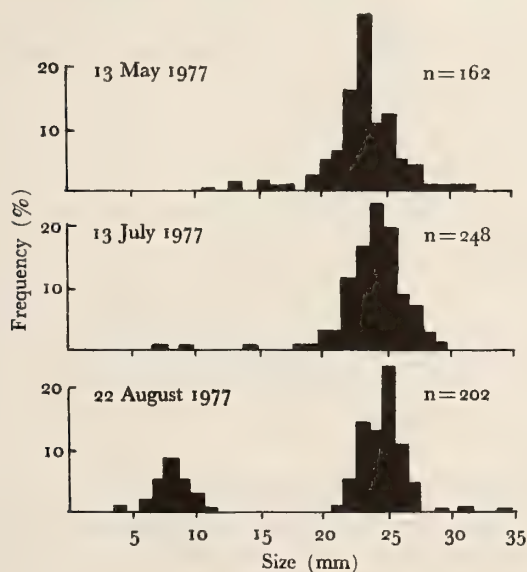


Figure 3

Size frequency histogram of *Cerithidea californica* in a representative pan at Principal Study Site. Juvenile dispersal is inferred from the appearance of a cohort of one-year old snails in August.

exposed may have been much higher, especially when snails were left completely dry, and exposed to full sunlight while lying on the dried bottoms of the pans. Snails from both Bolinas and San Francisco Bay were able to withstand immersion in sea water at 40° C for as much as 4 hours in both winter and summer with little indication of mortality (Figure 4). This temperature was well above the highest summer temperature recorded in the field (34° C) during the two years of monthly sampling.

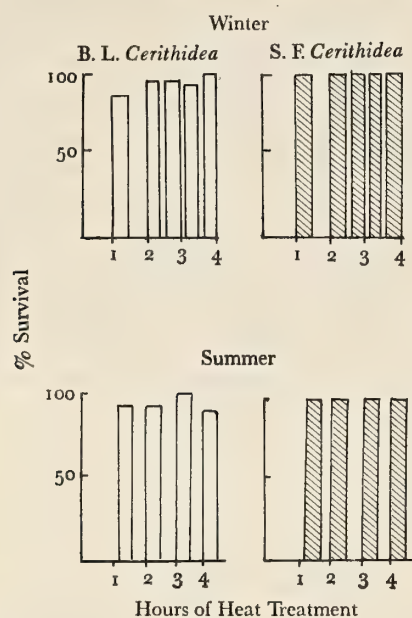


Figure 4

Summer and winter survival of *Cerithidea californica* following heat treatment (40° C) of different duration. Bolinas Lagoon vs. San Francisco Bay snails. Control snails had 100% survival in both summer and winter.

c. Desiccation

The tolerance of *Cerithidea* to desiccation was tested by checking for survival after different lengths of exposure to dry conditions. All subsamples of both Bolinas and San Francisco *Cerithidea* had over 90% survival for exposures of up to 9 days in dry conditions (Figure 5). In all but one case, 50% or more of each subsample of snails from both bays survived exposures between 11 and 15 days and became active upon re-immersion.

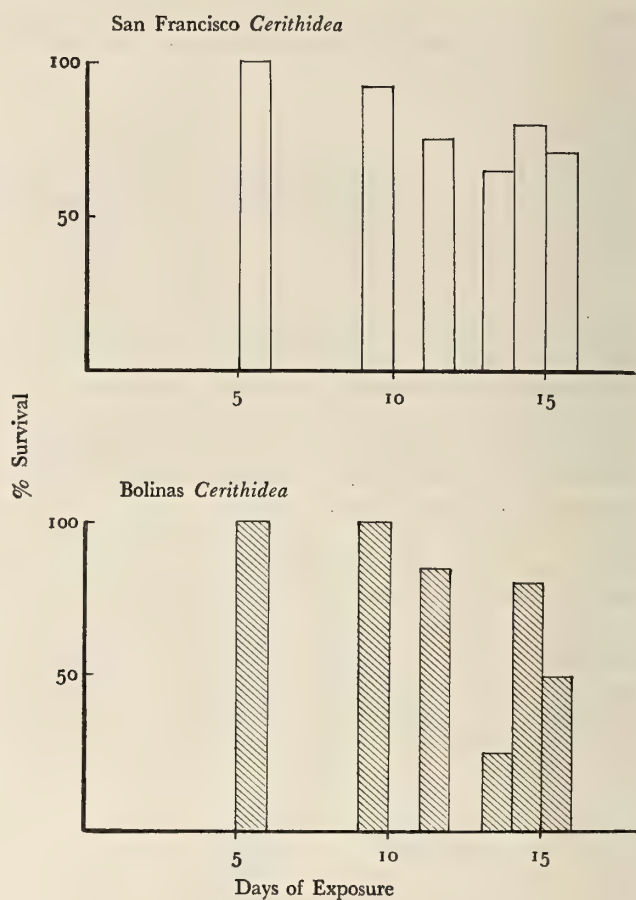


Figure 5

Survival of snails from Bolinas Lagoon and San Francisco Bay following different lengths of desiccation.

ACTIVITY PATTERNS, POPULATION FLUCTUATIONS AND MICROHABITAT UTILIZATION

Cerithidea californica in San Francisco Bay spends its entire winter in a dormant state beneath the canopy of *Salicornia* vegetation at the edges of the pans. The onset of cooler temperatures between September and November signals the migration of snails to overwintering habitats (Figure 6). From November to March high densities of snails remain retracted within their shells on the mud

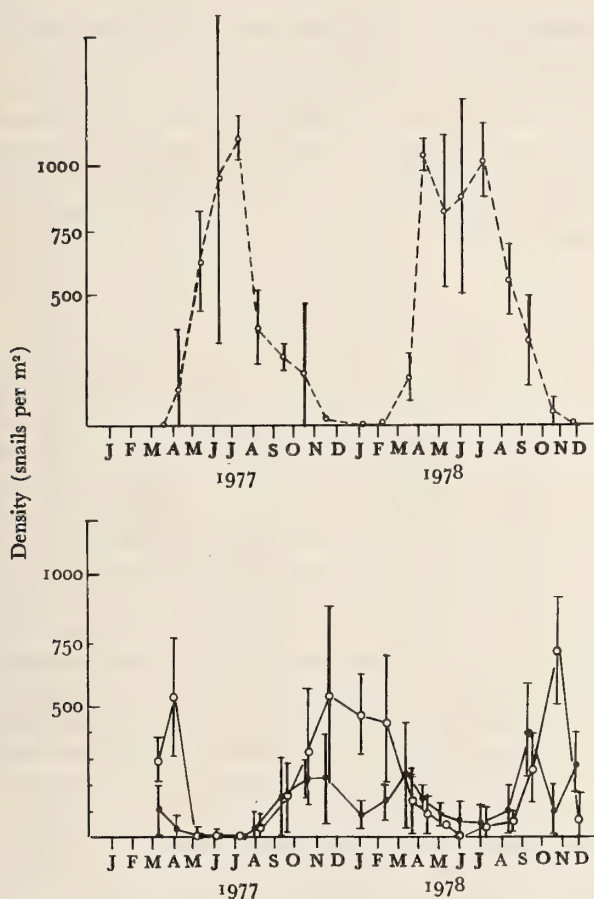


Figure 6

Seasonal changes in density of *Cerithidea californica* at a representative pan station at the Principal Study Site.

Upper graph: density in pan, mean \pm 2 S.E.

Lower graph: density in edge habitats. ● = North facing pan edges in *Salicornia*. ○ = South facing pan edges in *Salicornia*. Mean \pm 2 S.E.

above the reach of all but the highest tides [at or above mean higher high water (MHHW)]. Density of snails on the south-facing edges of the pan during the winter were greater than those on the opposite side for both years of sampling. The south-facing side of the pan had a gently sloping bank that received more sunlight and warmth during the cold winter months. In spring, *Cerithidea* becomes active again, migrating to the open pans filled with warm-

ing water. It was not unusual to have densities of nearly 1000 snails per m^2 in the pans for several consecutive summer months. Snails were active in all light conditions, provided they were on moist substrate or in standing water. Adults and juveniles were found together and all age groups appeared to have similar activity patterns. Population size at the principal study site, as inferred from densities, was relatively stable over the two-year period.

When most snails were recolonizing pan habitats in the spring, others were dispersing into creeks and moving towards the mudflats. Creek stations closest to the main pan built up densities of dispersers first and only later did snails reach lower stations further from the pan. The fact that increases in densities occurred initially at stations closest to the pans was evidence that the main pan was the source for these colonizers. Mean densities of *Cerithidea* in the creeks never exceeded 250/ m^2 , much lower than in the nearby pans. Dispersing *Cerithidea* appeared normal in all other respects, however, including the depositing of egg cases.

GROWTH

Sizes of marked, recaptured snails during a two-year period were used to calculate seasonal growth rates of different sized *Cerithidea californica* in different habitats. Although no controls for the effect of caging were tested in creek and mudflat habitats, it was assumed that cages had a negligible effect because caged and uncaged snails in the pan habitats did not differ significantly in growth rates (2 factor analysis of covariance [ANCOVA], size as covariate, $P > 0.05$).

There was no significant difference between growth of snails in different habitats in the winter (November to March) (one factor ANCOVA, size as covariate, $P > 0.05$). In addition there was no significant size effect upon growth in wintertime ($P > 0.05$). Winter growth rates for all sizes of snails in all habitats were in the range of 0.1 mm or less, which is on the same order as measuring error alone (Figure 7a). Thus, the growth of *Cerithidea* is limited to summer warm periods of the year.

During summer snails grew at a rate dependent on initial size and habitat. There was a significant difference in growth rates for different sized snails (one factor ANCOVA, size as covariate, $P < 0.001$) between April and October, with highest growth rates for the smallest snails. In addition, there was a significant effect of habitat on growth rate ($P < 0.001$). Pairwise comparisons of growth rates by habitat indicated three significantly dif-

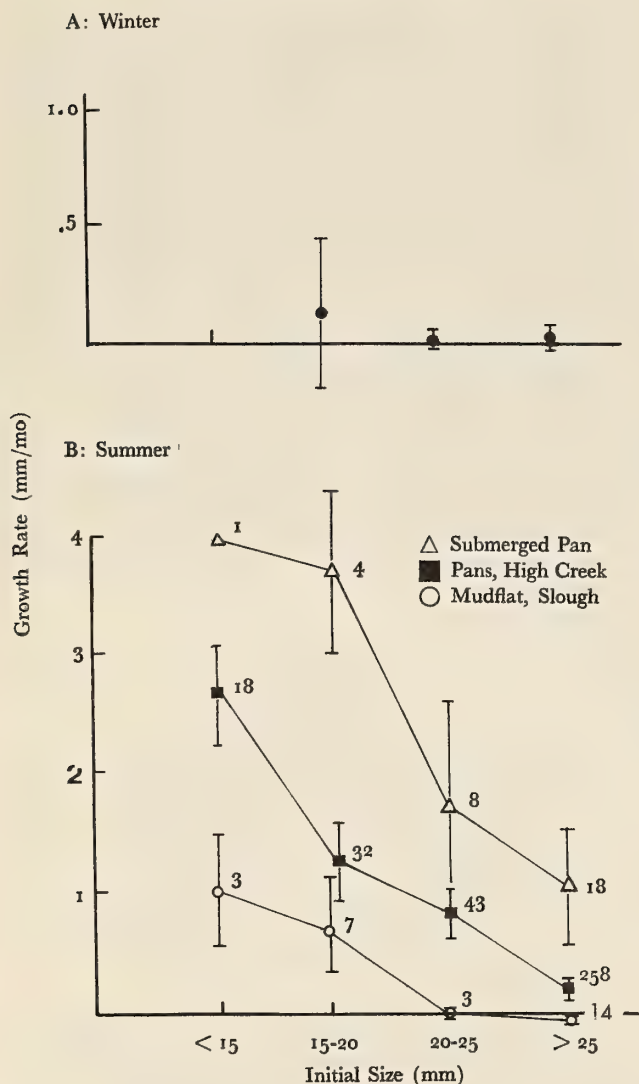


Figure 7

Growth rates of *Cerithidea californica* in different habitats. Mean ± 2 S. E.

A: Winter growth rates for all habitats combined.

B: Summer growth rates in three significantly different habitat groupings. Numbers indicate sample size.

ferent groups of habitats ($P < 0.05$). Growth data from these habitat groups were pooled for an analysis of mean summer growth rates by size category (Figure 7b).

Snails on mudflats and adjacent creeks (about 0.9 to 1.5 m above mean lower low water [MLLW]) grew slower

than snails in pans. Intermediate growth rates, indistinguishable from one another were observed in six habitats, five pans and one very high creek (2.1 to 2.4 m above MLLW). These intermediate growth rates are probably the normal growth rates for *Cerithidea* in San Francisco Bay because snails are found most often in these habitats. Highest growth rates were found in a single pan that was continuously submerged during nearly all of the experimental period.

COMPARISONS WITH OTHER BAYS

In the following comparisons, all information on populations outside of San Francisco Bay has been taken from studies by MACDONALD (1967), WHITLATCH (1972), DRISCOLL (1972), MCCLOY (1979) and RACE (1979). McDonald studied *Cerithidea* populations in Mugu Lagoon and Mission Bay in southern California, and San Quintín Bay and Black Warrior Lagoon in Baja California, Mexico. Most of his quantitative information is reported for populations in Mission Bay. McCloy conducted field studies at two locations in southern California; one in San Diego Bay at Chula Vista, CA, the other at Goleta Slough near Santa Barbara, CA. Northern California populations of *Cerithidea* were studied by Whitlatch in Tomales Bay at Millerton, CA; Driscoll at Drakes Estero, CA; and Race in Bolinas Lagoon, CA.

1. Differences in Habitat Utilization

Cerithidea californica usually occurs in creek beds, inner margins of mudflats and on the marsh surface, spanning a tidal range of about MLHW to MHHW (MACDONALD, 1967). In San Francisco Bay, it is restricted almost entirely to marsh habitats near the MHHW level, while tidal creeks and mudflats are occupied by the introduced mudsnail *Ilyanassa obsoleta*. At all sites studied in San Francisco Bay, *Cerithidea* colonized lower intertidal habitats each spring but were soon forced out of these areas by interactions with *Ilyanassa* (RACE, 1981). As a result, *Cerithidea* in San Francisco Bay occupy their full tidal range for only a month or two each year, and never reach normal summer densities in the lower habitats.

Other factors that may limit *Cerithidea* to a fraction of its habitat range in San Francisco Bay are the presence of an introduced isopod and long term human alterations to marsh habitat. In south San Francisco Bay, especially on the eastern shores, there is a lack of gently sloping mudflat at the edges of the marshes. Instead, there are abrupt drops in the marsh topography forming cliffs about 1 m in height that separate marsh from mudflat. These cliffs are formed

by the activities of an exotic burrowing and boring isopod, *Sphaeroma quoyanum* introduced into the bay from Australasia between 1850 to 1890 (CARLTON, 1979). By burrowing and making holes in the substrate at the edge of the marshes, this isopod has caused the weakening and subsequent wave erosion of many kilometers of shoreline. The result has been a decrease in the area of inner mudflat habitat adjacent to the marshes and suitable for *Cerithidea*. Snails are also limited by levees constructed at the shoreward faces of marshes which block access to the mudflats except through tidal creeks.

2. Differences in Behavior

The distinct seasonality of growth and activity for *Cerithidea* apparently occurs throughout its range. All records of egg cases in the field fall between May and November with peak abundances in June, July and August (MACDONALD, 1967; McCLOY, 1979; RACE, 1979). Snails are active and abundant on the marsh surface between about March and November. Snails from Mission Bay are chiefly nocturnal with daytime activity restricted to submerged or shaded situations (MACDONALD, 1967). *Cerithidea* in Tomales Bay is active during overcast days or in subdued light (WHITLATCH, 1972). Animals in San Francisco Bay were active under even full sunlight and sometimes on substrate that was only moist.

Winter hibernation occurs in all bays. In San Diego, Goleta Slough, Bolinas Lagoon and Drakes Estero, *Cerithidea* has been observed burrowed into the substrate during the winter. In San Francisco Bay, the majority of snails migrate from the pans and spend their winter on the surface of the marsh beneath a canopy of vegetation. A small number of San Francisco *Cerithidea* (< 5 per m^2) remain in the pans during winter, burrowing beneath the mud during cold weather, as seen in other bays. In Drakes Estero, Driscoll observed that *Cerithidea* burrowed into pan bottoms during the winter, but made no references to decreased abundances that might indicate a winter migration to different habitats. McCloy noted a winter depression of densities in San Diego Bay and suggested that many individuals migrate to higher levels of the creek bed during the winter. Because higher areas were outside his sampling plots, it is impossible to determine whether these animals overwinter by burrowing into the creek substrate or climbing out of water beneath the vegetation at creek's edge.

An intriguing behavioral difference was observed between animals from Bolinas and San Francisco during an experiment to determine the response of snails to the presence of *Ilyanassa*. In August 1977 about 300 Bolinas Lagoon snails were marked and released with equal numbers of marked San Francisco *Cerithidea* on one of the few

inner, wave protected mudflats near the principal study site. The response of Bolinas *Cerithidea* was significantly different than San Francisco snails (X^2 test, $P < 0.001$). Bolinas snails remained mainly in the creeks and on the mudflats, while San Francisco snails tended to return to higher intertidal habitats. Considering the poor dispersal capabilities of *Cerithidea* and the distance of open exposed coastline between these two locations, it would be interesting to study the degree of behavioral differences between bays, their ontogeny, and their possible adaptive significance.

3. Differences in Growth and Size

Every population studied in San Francisco Bay was dominated by animals in the 20 to 30 mm range, and animals larger than 30 mm could be found with ease. Mugu Lagoon, San Diego Bay and Bolinas Lagoon also had snails larger than 30 mm. In contrast, the largest snails in other bays were generally smaller. In Mission Bay animals exceeding 20 mm were scarce (MACDONALD, 1967). In Drakes Estero, snails rarely exceeded 24 mm (DRISCOLL, 1972). Size frequency data for Tomales Bay indicated few animals over 20 mm (WHITLATCH, 1972). It is unclear whether differences in growth rates or longevity have caused the dissimilarity in adult sizes between bays. Size and growth data provided by both McCLOY (1979) and MACDONALD (1967) suggest that growth rates for juveniles in San Diego and Mission Bay are the same as rates for similar sized snails in San Francisco Bay. By the time they are about 15 months old, young *Cerithidea* in all bays are about 15 mm. Both MacDonald and McCloy reported near zero growth rates for individuals over 20 mm in their studies. By comparison, individuals between 20-25 mm in San Francisco Bay grew, on the average, about 1 mm per month during the summer. Individuals greater than 25 mm grew slower, although they too exhibited positive growth rates during the summer. Because growth rates in San Francisco Bay were shown to be habitat dependent, it is uncertain whether the lower growth rates observed in other bays can be explained by habitat differences or actually reflect differences in growth rates between bays.

4. Differences in Reproduction and Development

Size of first reproduction for San Diego snails was reported as greater than 20 mm (McCLOY, 1979), similar to that seen in San Francisco Bay (22 to 24 mm). Egg case lengths reported for Mission Bay *Cerithidea* ranged from 25 to 85 mm, with 12 to 15 eggs per mm (MACDONALD, 1967). Egg cases in San Francisco Bay were considerably longer, ranging from 10 to 170 mm ($\bar{X} = 69$, $n = 355$),

with 11 to 33 eggs per mm (\bar{X} = approximately 18 mm). Sizes of eggs reported for both bays were the same, and were measured at approximately 0.2 mm in diameter.

Densities of egg cases and juveniles in Mission and San Diego Bays were highest in lower intertidal habitats. Maximum densities of egg cases were found on protected mudflats and in the *Spartina* zone (below MHHW), while juveniles were more abundant in creek habitats. In both bays egg cases and juveniles were present in marsh pan habitats, but in low densities (MACDONALD, 1967; McCLOY, 1979). In San Francisco Bay, egg cases and juveniles occur almost entirely in marsh pans. These younger stages were found in creeks or mudflat habitats only during the short time each year when *Cerithidea* colonized lower habitats. The differences in egg case and juvenile abundance in the lower habitats of San Francisco Bay result from interactions with the deposit feeding snail, *Ilyanassa obsoleta* (RACE, 1981), and probably do not reflect differences in natural history between bays.

5. Causes of Mortality

Predation by shorebirds, and to a lesser degree by grapsid crabs, were reported as significant causes of mortality for *Cerithidea* in San Diego Bay and Goleta Slough. Algal smothering was also noted as an important periodic cause of mortality for snails (McCLOY, 1979). Because *Cerithidea* in San Francisco Bay inhabits only higher intertidal habitats in the marsh, it has been relieved to a large degree from both crab and bird predation as adults. Mortality from algal smothering is patchy in both time and space, and has been observed in San Francisco Bay mainly in pan habitats in late summer. Increased algal growth may also cause mortality by rafting both small and large snails away from pans and stranding them high and dry atop the *Salicornia* canopy when the tides recede. Because juveniles are less able to withstand desiccation stress (McCLOY, 1979), it is likely that mortality by rafting falls heaviest on small sized snails.

Another source of mortality, unique to San Francisco Bay, is predation by *Ilyanassa obsoleta* on the eggs and juveniles of *Cerithidea* (RACE, 1981). While *Ilyanassa* is not a direct cause of mortality for adult *Cerithidea*, the behavioral avoidance of *Ilyanassa* by *Cerithidea* adults exposes them to possible death from desiccation if they are forced to remain in dry habitats at the creek's edge for long periods of time (RACE, 1981).

Mortality in San Francisco Bay is also caused by habitat loss from physical disturbances. During the period of this study, many pans disappeared, filled in by the advancing

growth of *Salicornia* or buried under wavewashed driftwood and debris. It is not known how much mortality is caused by these irregularly occurring physical disturbances. Driftwood can also act as a dispersal agent for any snails that are on a piece of wood that floats away.

Observations in this and other studies (MARTIN, 1972; YOSHINO, 1975; Sousa, personal communication) have indicated that *Cerithidea* is the host to parasitic infections by larval trematodes. Trematode infections castrate adult snails and may cause increased mortality either in a direct manner or indirectly by reducing a snail's tolerance to physiological stress (VERNBERG & VERNBERG, 1963).

SUMMARY

Cerithidea californica in San Francisco Bay has life history characteristics that are similar to other populations along the Pacific coast. Some differences between bays were found in overwintering behavior, habitat utilization and adult size. Populations of *Cerithidea* in San Francisco Bay are threatened by at least three factors: human habitat destruction, biotic habitat alteration, and competitive interactions. *Cerithidea* now occupies only a fraction of the area it did just one hundred years ago. Because of its sedentary lifestyle and limited dispersal, *Cerithidea* is not able to easily recolonize areas following local extinctions, especially where marshes have been separated or blocked by the construction of levees. Exotic species introduced into the bay within the last century further compound problems for *Cerithidea*. The burrowing and boring activities of the *Sphaeroma quoyanum* from Australasia have reduced the marsh-mudflat interface to a cliff topography, further limiting the amount of suitable mudflat habitat for *Cerithidea*. Finally, competitive interactions and predation by the introduced mudsnail *Ilyanassa obsoleta* restrict *Cerithidea* to marsh pan habitats for most of the year.

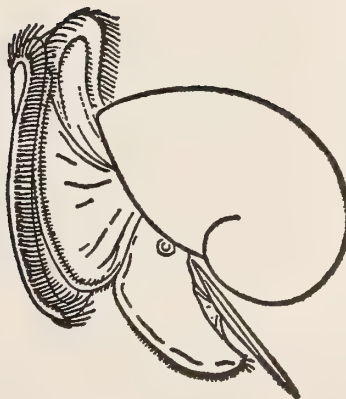
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Reproductive Biology of *Colus stimpsoni*

(Prosobranchia : Buccinidae)

IV. Oogenesis¹

BY

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(5 Plates; 1 Text figure)

INTRODUCTION

SINCE WILSON SUGGESTED in 1896 (cited in WILSON, 1925) that embryogenesis begins in oogenesis, biologists from many disciplines have been attracted to the development of female gametes. Present knowledge concerning oocyte development and its subsequent activities following activation by the sperm indicate that large amounts of genomic information, in addition to food reserves, are stored during oogenesis. It is also clearly indicated that certain cytoplasmic areas of the egg contain factors which may activate or modify certain genomic activities early in development (DAVIDSON, 1976).

Early studies on the development of various invertebrates indicate that two categories of eggs exist: regulatory and mosaic. Further, regulatory eggs exhibit radial cleavage patterns; whereas, mosaic eggs generally exhibit spiral cleavage patterns. The phenomena of spiral cleavage and mosaicism provide unique morphological markers for following the fate of blastomeres, but, more importantly, each blastomere has restricted developmental potentials which are established during oogenesis (WILSON, 1925; RAVEN, 1961; CATHER, 1971; DAVIDSON, 1976). The mo-

lecular events establishing the patterns of cytoplasmic localization, however, are poorly understood (DAVIDSON & HOUGH, 1972; DAVIDSON, *op. cit.*). It is therefore clear that a better understanding of both ultrastructural and molecular events of oogenesis are essential to comprehend the relation between oocyte organization and development.

Many neogastropods, in addition to possessing mosaic development, exhibit the phenomenon of nutritive eggs (THORSON, 1935, 1940; DUPOUY, 1964; RADWIN & CHAMBERLIN, 1973; LYONS & SPIGHT, 1973; SPIGHT, 1976). These eggs ("nutritive eggs" or "nurse eggs") are otherwise normal female germ cells but abort in early development or embryogenesis and serve as food for the developing young within a common spawn capsule. The causal factors involved in nutritive egg determination have been suggested to reside in atypical sperm (PORTMANN, 1926, 1927, 1930; HYMAN, 1925) or in properties of the egg (DUPOUY, 1964; STAIGER, 1950; BURGER & THORNTON, 1935). Since atypical sperm are reported to be incapable of participating in egg-penetration or amphimixis (STAIGER, 1951; THOMPSON, 1973), the factors involved in nutritive egg development and determination in neogastropods remain obscure. The present study concerns some ultrastructural and cytochemical aspects of oogenesis in the neogastropod *Colus stimpsoni* (MÖRCH, 1867) to elucidate some of the events of oogenesis and the nutritive egg phenomenon.

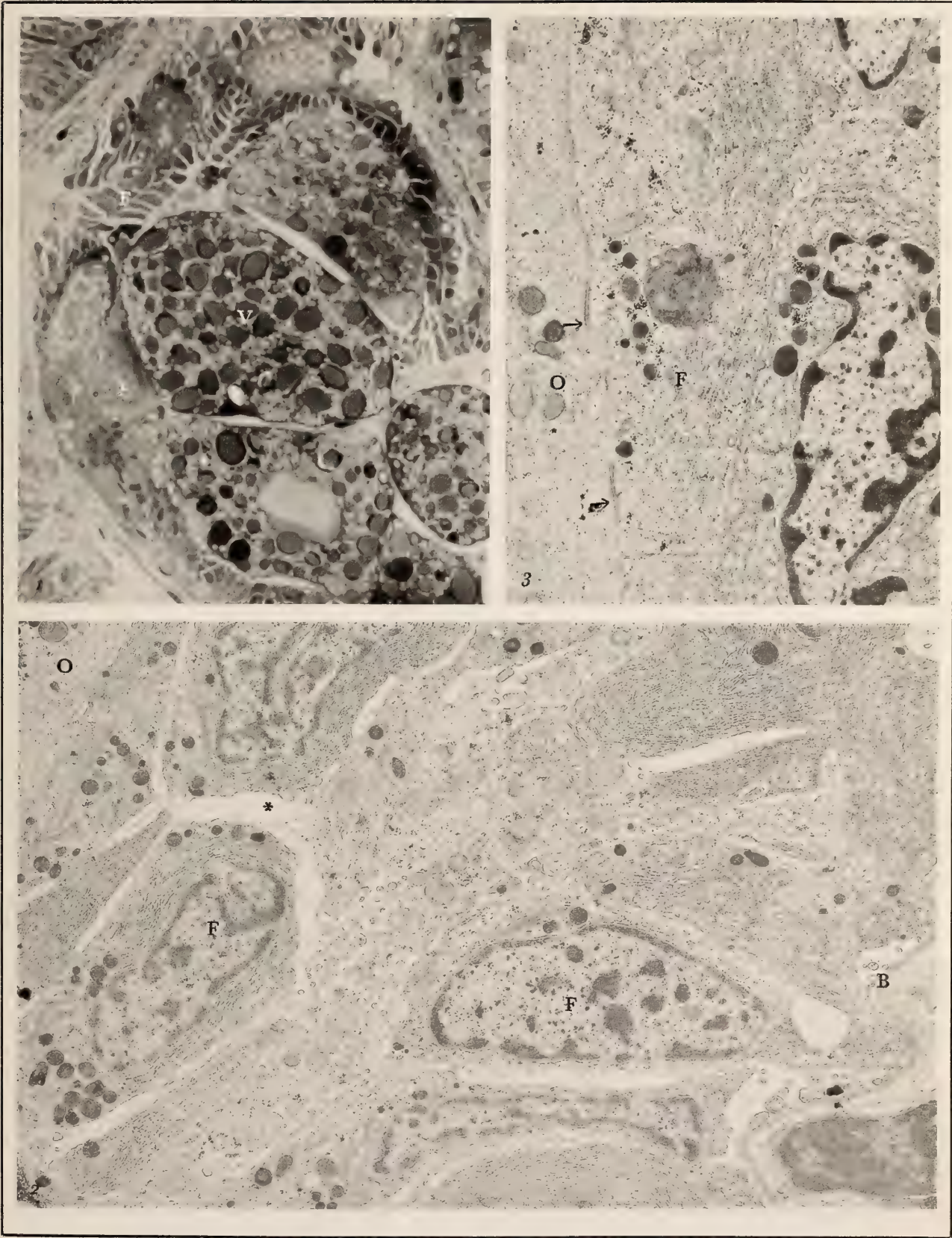
¹ Contribution No. 95 from the Marine Science Institute, Northeastern University

Explanation of Figures 1 to 3

Figure 1: Thick epon cross section of an ovarian tubule. Follicle cells (F) delineate the tubule with oogonia and early oocytes (E) interspersed among follicle cells. Vitellogenic (V) and postvitellogenic oocytes occur within the luminal region of the tubule. $\times 500$

Figure 2: Section through peripheral region of ovarian tubule. B - basal lamina F - follicle cell O - early oocyte; note material within intercellular space (*) $\times 7500$

Figure 3: Follicle cells (F) adjacent to oocytes (O) have desmosomes (arrows) along their borders and are flattened $\times 13500$



MATERIALS AND METHODS

The procedures employed in this study were in accordance with those reported in the first papers of this series (WEST, 1978a, 1978b). For ultrastructural localization of carbohydrates, the periodic acid-silver methenamine (PASM) technique was employed. Sections were collected on stainless steel grids and oxidized for 6 to 8 minutes with 1% periodic acid; control sections were not oxidized. Sections were washed for 30 minutes, exposed to silver methenamine (PEARSE, 1972) for 30 minutes at 60°C and subsequently processed according to PEARSE (*op. cit.*). Grids with sections were coated on drops of the various solutions.

OBSERVATIONS

The organization and histology of the female reproductive system were considered in detail in the third paper of this series (WEST, 1979) and only the salient features will be considered here. The ovary consists of numerous branching tubules which join to form the single oviduct passing along the columellar side of the visceral mass as the renal oviduct. The thin-walled renal oviduct enlarges and becomes glandular at the posterior limits of the mantle cavity giving rise to the pallial oviduct. The pallial oviduct, which passes along the roof of the mantle cavity, constitutes the largest part of the oviduct and consists of three parts: a glandular region, the bursa copulatrix and the vagina. The glandular region is histologically similar along its length but has two differentially staining regions which correspond to an albumin gland and a capsule gland. There is no discernible ingesting gland nor a seminal receptacle within the pallial oviduct in *Colus stimpsoni*.

Ovarian tubules are separated from each other by a 2 to 8 μm thick layer of loose connective tissue and, occasionally, a few muscle fibers and pigment cells. Follicle cells, oogonia and young oocytes lie on the periphery of tubules, subjacent to the basal lamina, with vitellogenic and postvitellogenic oocytes generally situated in the luminal portion of the tubules (Figure 1). Oogenesis is unsynchronized within tubules and, thus, nearly all stages of oocyte development may be observed in histological section.

Oogonia are irregularly clustered on the tubule periphery surrounded by follicle cells and young oocytes; mitoses of gonial cells are occasionally encountered. As oogenesis begins, gonial cells give rise to primary oocytes which are usually in clusters of 2 to 6 cells. These oocytes are eventually separated from each other by an interrupted encapsulating layer of follicle cells. During vitellogenesis,

as the oocyte increases in size, follicle cells retreat from the oocyte surface, beginning on the luminal-facing surface, ultimately leaving postvitellogenic oocytes free in the tubule lumen. Occasionally, during late vitellogenic phases, follicle cells remain scattered over the oocyte surface and appear as a thin, broken, squamosal-like layer.

Follicle Cells

Follicle cells form a layer 3 to 4 cells thick on the periphery of ovarian tubules and rest on the basal lamina (about 0.5 μm thick) which is composed of a dense aggregate of collagenous-like fibers. Within this peripheral layer, follicle cells vary in shape from columnar to cuboidal (Figure 2). However, they become flattened and rather thin in cross section as they and their associated oocytes move toward the tubule lumen (Figure 3). The polymorphic nucleus occupies most of the cell volume (Figure 2), and the cytoplasm is dominated by a well developed rough endoplasmic reticulum and the Golgi complex. The cytoplasm also contains numerous, Golgi derived, electron-dense inclusions, and, occasionally, a few large lipid droplets, glycogen particles and residual bodies (Figures 2 and 3). Cisternae of the Golgi complex, as well as the endoplasmic reticulum, are filled with an electron-dense homogeneous material (Figure 3). Mitochondria are scattered throughout the cytoplasm but are more numerous in the cortical region of the cell. Adjacent follicle cells have desmosomes irregularly distributed along their borders. Activities and changes occurring within follicle cells will be considered below in conjunction with the stages of oogenesis.

Oogenesis

Previtellogenic oocyte: In the earliest previtellogenic oocytes observed, the nucleus is irregular in outline, and the chromatin is granulofibrillar with small clumps irregularly distributed throughout the nucleoplasm; occasionally a few clumps of chromatin are appressed to the inner aspect of the nuclear envelope (Figure 4). The nucleolus is heterogeneous and eccentrically situated near the nuclear envelope which is studded with ribosomes and irregularly perforated by a few nuclear pores. The moderately electron-dense ooplasm contains abundant free ribosomes and a number of cisternae of rough endoplasmic reticulum, several of which are in concentric perinuclear bands. Mitochondria are randomly distributed and present a variety of configurations ranging from round to "horseshoe" shapes in profile. Frequently "doughnut"-shaped mitochondria are encountered in which the internal mem-

brane limited areas contain a finely granular or filamentous material (Figure 4). These "doughnut"-shaped profiles may represent various sectional planes through the "horseshoe"-shaped mitochondria since the cytoplasmic regions enclosed within the concave surfaces are very similar to the internal membrane limited regions of the "doughnut"-shaped mitochondria (Figure 4); this suggests a possible cup-shaped 3-dimensional configuration. A few stacks of flattened, occasionally concentric, Golgi cisternae are irregularly distributed throughout the ooplasm.

Previtellogenic oocytes are generally clustered in groups of 2 to 6 adjacent to early vitellogenic oocytes. Prior to the onset of vitellogenesis the oocyte increases to about $40\ \mu\text{m}$ in diameter. The nucleus swells to about $30\ \mu\text{m}$ in diameter, filling almost the entire cell volume, and assumes a subspherical shape (Figure 5). The nuclear envelope is perforated by a few pores, and its outer surface is studded with ribosomes. Coarsely granular chromatin is randomly distributed within the nucleoplasm with fine, filamentous chromatin distributed between the granular material. The nucleolus increases to about $10\ \mu\text{m}$ in diameter and has Feulgen-positive material adhering to its outer boundary. Numerous mitochondria are randomly distributed throughout the ooplasm and vary in shape from round to rod-shaped, occasionally branched, in profile. Areas of the ooplasm contain aggregates of glycogen particles, and there is an apparent increase in abundance of endoplasmic reticulum (Figure 5). The ground substance is somewhat less electron-dense than in earlier oocytes. The oolemma is smooth in profile, and no intercellular bridges have been observed. Follicle cells are appressed to the oocyte in regions not in contact with other oocytes and are flattened (Figure 3). Desmosomes are distributed randomly along the adjacent follicle cell-oocyte membranes (Figure 3); occasionally these junctions are rather extensive.

Vitellogenic Oocytes: During the vitellogenic phase of oocyte development, three major events simultaneously occur: (1) a dramatic increase in the number of organelles, (2) changes in the morphology of the oolemma, and (3) vast accumulations of food reserves. These reserves are in the forms of both lipid and proteid yolk inclusions and also extensive aggregations of glycogen particles.

At the onset of vitellogenesis, the oocyte increases in size, measuring about $40\ \mu\text{m}$ in diameter, and the nucleus becomes irregular in outline (Figure 6). Throughout the remainder of the vitellogenic phase, the oocyte increases in size, but the nucleus only increases slightly, to about $50\ \mu\text{m}$ in diameter. There is a dramatic increase in the number of nuclear pores, concomitant with nuclear size increase, but they remain fairly constant throughout the remainder of the vitellogenic phase. These pores are about $5\ \text{nm}$ in diameter and vary from 30 to $50\ \text{nm}$ apart. The outer surface of the nuclear envelope is decorated with ribosomes, but they appear less densely aggregated than in earlier phases of development. The nucleolus increases to about $12\ \mu\text{m}$ in diameter and is basophilic, but during late stages of vitellogenesis it becomes surrounded by an acidophilic region, resulting in a nucleolus embedded in a large (about $20\ \mu\text{m}$ in diameter) amphinucleolus. Occasionally one or two small accessory nucleoli are encountered. Early in vitellogenesis, there is a dramatic increase in the number of mitochondria, and they present a variety of profiles ranging from elongate rods to dumb-bell shapes (Figure 6). They are initially situated in perinuclear clusters but are eventually distributed randomly throughout the ooplasm. There is also an apparent increase in the abundance of endoplasmic reticulum.

In early vitellogenesis changes occur in the oolemma beginning on the luminal surface. Initially, follicle cells

Explanation of Figures 4 to 10

Figure 4: Early previtellogenic oocytes. Arrows - "horseshoe" - "doughnut" shaped mitochondria

× 6 700

Figure 5: Previtellogenic oocyte

× 6 700

Figure 6: Early vitellogenic oocyte. The oolemma forms microvilli on the luminal surface with small pits and vesicles (arrows) subadjacent to the oolemma in the microvillar regions. Note material in intercellular spaces formed as follicle cells retreat from oolemma (*). N - nucleus

× 13 600

Figure 7: Prolipoid bodies. Note the concentric and irregular bands of electron-dense material. Small prolipoid bodies (arrow) may fuse, forming larger bodies.

× 20 000

Figure 8: Regions of prolipoid bodies react strongly to the periodic acid-silver methenamine technique indicating the presence of a carbohydrate. Note bands (arrow) of PASM positive material within the bodies.

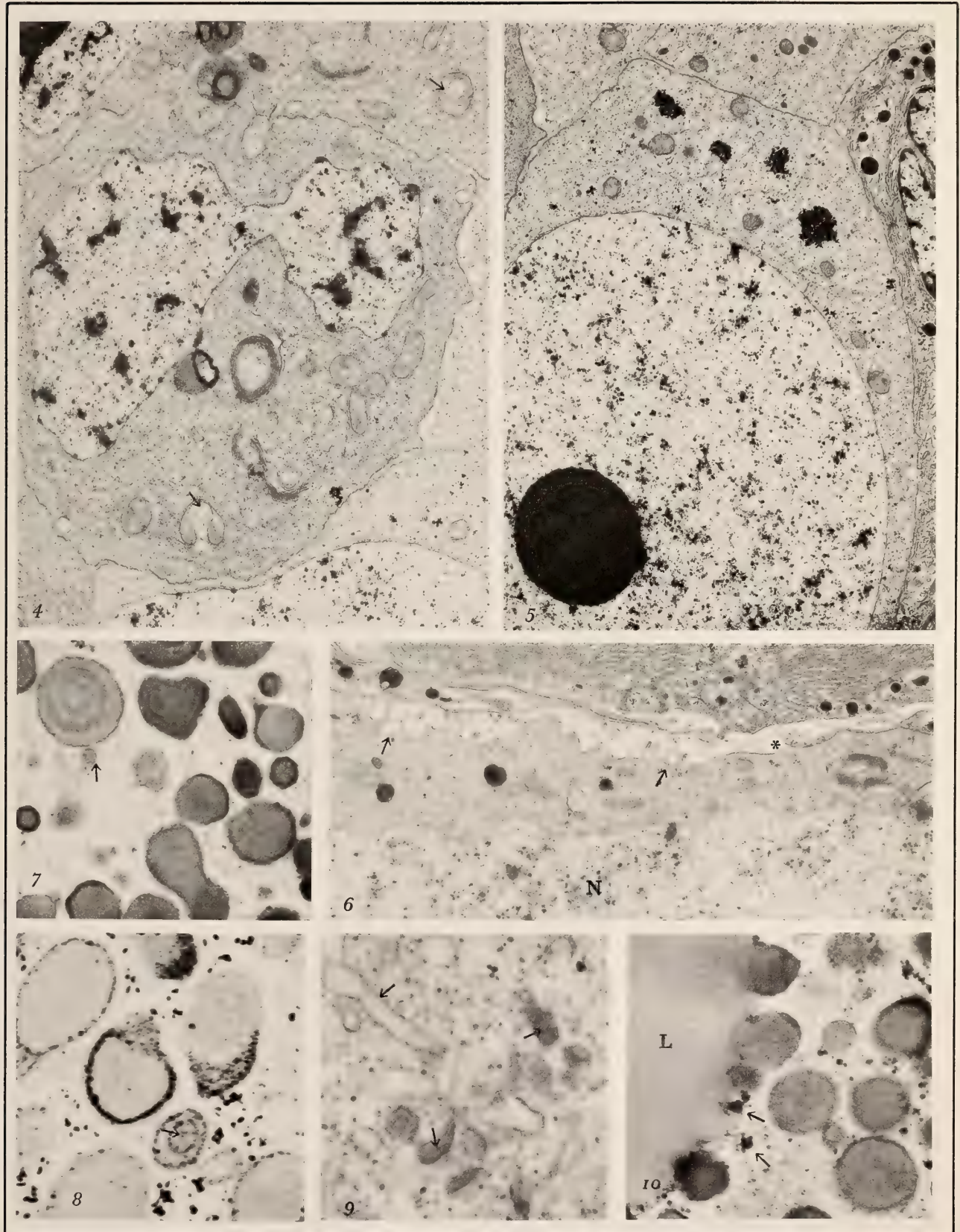
× 32 000

Figure 9: Endoplasmic reticulum is involved in prolipoid body formation. Cisternae contain electron-dense material and undergo vesiculation or dilation, or both (arrow), forming prolipoid bodies.

× 41 000

Figure 10: Prolipoid bodies fuse, forming lipid yolk droplets (L) surrounded by carbohydrate material (arrow)

× 20 000



are appressed to the oolemma with desmosomes irregularly distributed along the appressed membranes (Figure 3). On the luminal surface, which also establishes the animal pole, the oolemma is thrown into folds and bears microvilli (Figure 6). Also, the ooplasm subjacent to this region contains a few small vesicles, probably endocytotic. Throughout vitellogenesis, the oolemma progressively forms microvilli until the entire oolemma becomes microvillar (see Figure 12). Microvilli are simple, occasionally branched (about $0.2\ \mu\text{m}$ in diameter) with a moderately electron-dense filamentous material distributed between them.

Synthesis and deposition of yolk materials is signaled by the appearance of clusters of electron-dense bodies and lipid droplets. Lipid yolk deposition appears to be initiated first, followed by proteid yolk. This sequence is suggested since lipid yolk is evident in micrographs of early vitellogenic oocytes but proteid yolk is not. Glycogen accumulations apparently occur throughout vitellogenesis. Deposition of lipid yolk (phospholipids, lipids, and lipoproteins) begins with the accumulation of clusters of electron-dense bodies (prolipoid bodies). Prolipoid bodies (Figure 7) are membrane limited and contain heterogeneous material. This material varies in electron density with concentric or irregular bands of electron-dense material distributed within a finely granular matrix. The matrix appears lipid in nature, but the banded component reacts strongly to the PASM technique suggesting a carbohydrate moiety (Figure 8).

Prolipoid bodies appear to be derived from both smooth and rough endoplasmic reticulum (Figure 9). Cisternae of the endoplasmic reticulum, which are distributed in loose concentric arrays in regions of prolipoid body accumulations, are dilated and contain finely granular material (Figure 9). In some instances the cisternae have enlarged, bulbous regions. Prolipoid body formation apparently occurs in two ways. Cisternae may either vesiculate forming small spherical bodies, or constrict at various intervals forming elongate irregularly shaped prolipoid bodies (Figure 7). The smaller spherical bodies may subsequently fuse forming the larger prolipoid bodies or they may fuse with existing prolipoid bodies. Lipid yolk is formed by fusion of prolipoid bodies (Figure 10). Following fusion the contents undergo rearrangement forming a large sudanophilic lipid droplet surrounded by a carbohydrate-rich material, probably glycogen (see Figure 25). Lipid material is subsequently added by fusion of prolipoid bodies, and the lipid yolk inclusion increases in size. Evidence also suggests that material derived from the endoplasmic reticulum is added to lipid yolk. This is indicated by short, discontinuous cisternae of endoplasmic reticulum distributed in a concentric array partially enclosing lipid yolk.

Proteid yolk inclusions appear after the initial deposition of lipid yolk (Figure 11). With the onset of proteid yolk deposition there is an increase in the number of Golgi bodies with a subsequent dramatic increase in the number of cytoplasmic vesicles (Figure 12). These vesicles (Figure 13) appear to be one of three types: one derived from blebbing and vesiculation of the rough endoplasmic reticulum (Figure 14), one type derived by endocytotic activity of the oolemma (Figures 12 and 15), and a third type derived from the Golgi complex. Vesicles derived from the endoplasmic reticulum contain a moderately electron-dense flocculum which primarily adheres to the limiting membrane (Figures 13 and 14). Endocytotic vesicles also contain a moderately electron-dense flocculum adhering to the inner surface of the limiting membrane and, in addition, a smaller (50 nm in diameter) dense-cored vesicle or particle (Figures 13 and 15). The core particle reacts positively to PASM procedures and is very similar to the particles found in the intercellular spaces between follicle cells and the oocyte (Figure 15). These two types of vesicles are similar in size (20-40 nm in diameter) and configuration, with the exception of the dense-cored particle of endocytotic vesicles. Because of the likeness of these two types of vesicles, the particle within some vesicles may represent a sectioning artefact. However, because of similarities of the intercellular material, some vesicles are interpreted as being endocytotically derived. Golgi-derived vesicles contain a homogeneous, electron-dense material and range in size from 0.75 to 1 μm in diameter. Proteid yolk deposition is initiated by the fusion of these various vesicles. The combined material undergoes reorganization, with the resulting vesicle (yolk vesicle) containing a fine, granulofibrillar material (Figure 16). Yolk vesicles fuse forming larger intermediate yolk vesicles, and the contained material of these vesicles condenses forming electron-dense, short fibrous material. This fibrous material further condenses into the homogeneous electron-dense proteid yolk platelet (Figure 17). Proteid yolk platelets increase in size by additional fusion of yolk vesicles, or by fusion of the three types of vesicles directly to the platelet. Material added via the Golgi complex is associated with the endoplasmic reticulum (Figure 18). Endoplasmic reticulum juxtaposed to the forming face of the Golgi complex blebs off small vesicles which apparently fuse with the Golgi lamellae (Figure 18). Proteid yolk platelets vary in size from 3 to 8 μm in diameter and are oval to spherical in shape (see Figures 23 and 24). These platelets are bipartite with a large homogeneous core and a thin outer region (see Figure 24). This outer cortical region varies in thickness and reacts strongly to the PASM technique indicating the presence of a carbohydrate (Figure 19).

The homogeneous core does not react to the PASM procedure; however, the highly crystalized nature of the material may interfere with the reaction.

Other Cytoplasmic Features: The ooplasm contains a variety of inclusions, including residual and multivesicular bodies. Microtubules appear within the ooplasm during early vitellogenesis (Figure 13) and are randomly arrayed throughout the ooplasm, but they appear more dense in the cortical region. Clusters of finely granular, electron-dense material appear in early vitellogenesis (Figure 11). These aggregates are distributed in large fiber-like arrays (Figure 11, insert) irregularly within the ooplasm, and, presumably, are of nuclear origin ("nuage"). Annulate lamellae consisting of 6 to 10 parallel stacks of short (about 3 μ m in length) lamellae appear in late- and post-vitellogenic oocytes.

During microvilli formation on the oocyte membrane, interfacial clefts form between follicle cells and the oolemma in the region of microvilli (Figure 6). These clefts progressively increase in size, with increased microvilli formation, and the intercellular spaces thus formed contain heterogeneous material. Follicle cells in the vicinity (up to 3 to 4 cells distance) of oocytes, but not tightly appressed to them, have fairly large intercellular spaces (Figure 2). These spaces contain glycogen particles, heterogeneous granular to flocculent material and small flocculum-filled vesicles (Figures 20 and 21). The intercellular material is apparently released by follicle cells through exocytosis and by blebbing (Figures 20 and 21). The intercellular space between late- and post-vitellogenic oocytes and follicle cells contains fairly large accumulations of glycogen particles (Figure 22). Presumably these particles accumulate because late- and post-vitellogenic oocytes no longer incorporate the intercellular material.

Postvitellogenic Oocytes: Following vitellogenesis, oocytes are 180 to 190 μ m in diameter (Figure 23). The nucleus (germinal vesicle) is subspherical, about 50 μ m

in diameter, and the nuclear envelope has many shallow indentations and finger-like extensions (Figure 24). It is generally situated just beneath the luminal surface of the oocyte, establishing the animal pole. The nucleolus is about 10 μ m in diameter within a larger, about 20 μ m diameter, acidophilic amphinucleolus (Figure 23). There is a small region of ooplasm surrounding the nucleus which is relatively free of cellular inclusions. The oolemma bears numerous simple, occasionally branched, microvilli (Figure 22) which have electron-dense tips. The vitelline envelope is moderately electron-dense and filamentous. The ooplasm is dominated by yolk inclusions (Figures 23 and 24) and aggregates of glycogen particles which occasionally occupy extensive areas, particularly in the vegetal pole (Figure 25). Mitochondria are randomly distributed within the scanty cytoplasm and are rod-shaped. A few Golgi bodies and short cisternae of endoplasmic reticulum are irregularly distributed in the ooplasm. A few ooplasmic vesicles remain and are more abundant in the cortical region (Figure 22). However, no cortical granules have been observed. Residual bodies and annulate lamellae are occasionally encountered. Figure 26 summarizes the morphological changes in the oocyte during oogenesis.

Cytochemistry

Lehman's polychrome procedure and specific cytochemical tests suggest the presence of a number of macromolecular groups within the ovary and oocytes. Proteid yolk is predominantly neutral proteins but also retains alkaline fast green suggesting these proteins are moderately rich in basic amino acids. These yolk platelets also react positively to PAS and PASM indicating the presence of a carbohydrate moiety. Lipoid yolk is sudanophilic and reacts weakly to the acid hematin test, suggesting that it contains lipids and phospholipids. The vitelline envelope is PAS positive, and from results of Lehman's polychrome procedure it is a mucopolysaccharide. Follicle cells stain intensely with bromphenol blue and Lehman's

Explanation of Figures 11 to 13

Figure 11: Early mid-vitellogenic oocyte. The nucleus is subspherical and the nuclear envelope is perforated by numerous pores (arrow). Lipoid yolk (L) deposition is initiated prior to small proteid yolk (P) platelet formation. Prolipoid bodies are clustered near lipoid yolk. Aggregates of electron-dense material ("nuage") are irregularly distributed (*).

× 6 700

Insert — aggregates of electron-dense material from fiber-like arrays

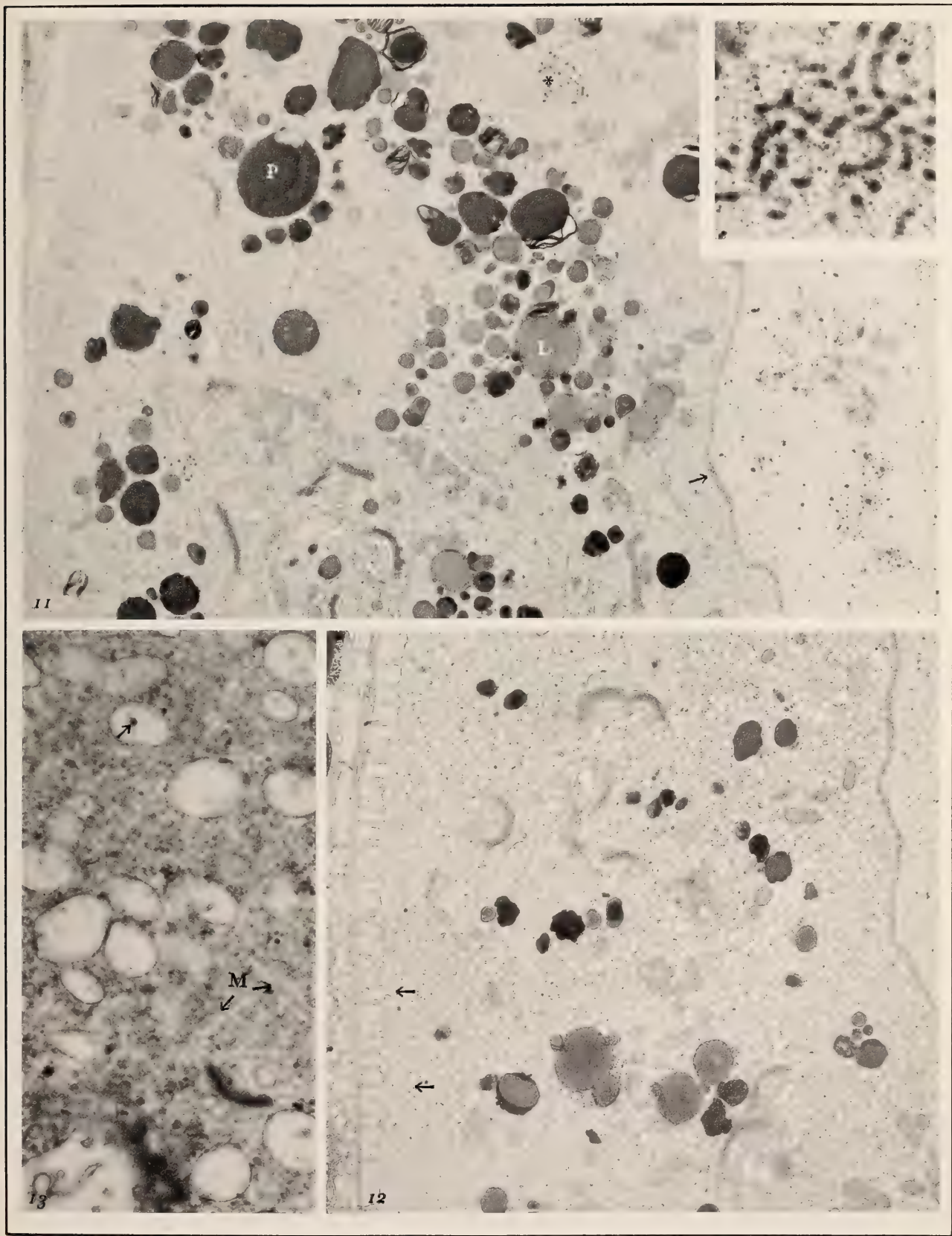
× 28 500

Figure 12: Mid-vitellogenic oocyte. Proteid yolk deposition is accompanied by numerous ooplasmic vesicles derived from endocytotic activity (arrows) and from vesiculation of endoplasmic reticulum.

× 6 700

Figure 13: Ooplasmic vesicles involved in proteid yolk formation. Some vesicles (endocytotic) contain an electron-dense particle (arrow). M — microtubules.

× 36 000



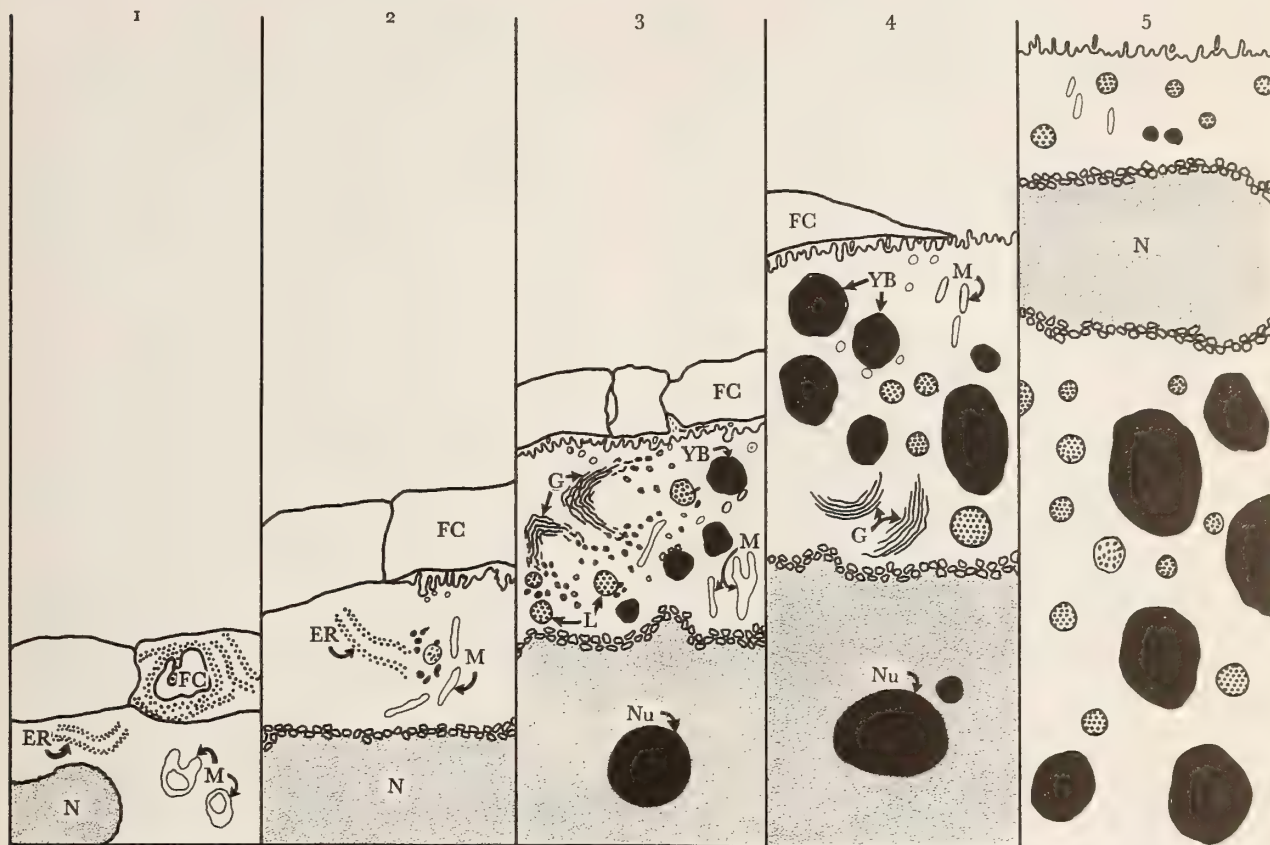


Figure 26

Diagrammatic representation of the sequence of events during oogenesis in *Colus stimpsoni*. 1 - previtellogenic oocyte; 2 -, 3 -, and 4 - vitellogenic phase; 5 -postvitellogenic oocyte.

ER - endoplasmic reticulum;
G - Golgi complex; L - lipoid yolk;
N - nucleus; Nu - nucleolus;

FC - follicle cell;
M - mitochondria;
YB - proteid yolk

polychrome indicating they are rich in proteins. Table 1 gives the results of specific cytochemical staining techniques.

DISCUSSION

Vitellogenesis: The female gamete is a highly specialized cell which must solve many of the physiological problems of insuring sufficient genomic information and nutritive substances for the rapid metabolic activities of the embryo. These activities are initiated with sperm activation of the ovum and extend until such time as the

embryo may begin transcription of its own genome and the larva begins feeding. The continuum of oogenesis is generally divided into three phases. The first phase, previtellogenesis, is usually signalled by the rapid increase in size of the nucleus, accompanied by synthesis of large amounts of RNA, and an increase in number of mitochondria. These activities may continue throughout oogenesis, but they provide the genomic information and metabolic machinery for the activities of the rapidly dividing embryo. The second phase, vitellogenesis, is morphologically delineated by accumulation of various food reserves. The last phase, postvitellogenesis, is relatively quiescent, lasting until activation by the spermatozoa.

Table 1

Results of cytochemical staining procedures of the ovary of *Colus stimpsoni*

Technique	Oocytes					Follicle cells
	Cytoplasm	Oolemma	Proteid Yolk	Lipoid yolk		
Acid hematin	—	—	—	+		±
Alkaline fast green	±	—	+	—		+
Bromphenol blue	+	—	++	—		+++
PAS	+++	++	+	+		+
			(outer region)	(outer region)		
Acid phosphatase	±	—	±	—		±
Alkaline phosphatase	±	—	±	—		±
Sudan IV	—	—	—	++		—

+, ++, +++ increasing degrees of positive staining intensity
 — negative reaction
 ± questionable results

HISAW (1963) noted that perhaps one of the first evolutionary problems of an ovum was that of providing adequate sources of energy for embryological development. In the primitive situation, the ovum must have been capable of accumulating sufficient food reserves through its own metabolic efforts but, very early, this task exceeded the capabilities of a single cell. The various food reserves accumulated by oocytes are commonly referred to as "yolk," but WILSON (1925) considered these nutritive sources as a secondary plasm, calling them "deutoplasm," and defined them as passive or lifeless protoplasmic components. The majority of investigations on oogenesis have paid particular attention to the vitellogenic phase, especially to the formation of those yolk bodies which contain a combination of protein and carbohydrate. Vitellogenesis,

thus, has been approached from a unilateral direction (reviews, ANDERSON, 1974; HUEBNER & ANDERSON, 1976).

The kinds and amounts of yolk vary considerably throughout the animal kingdom, and it is currently recognized that yolk production is dependent upon materials from inside or outside the oocyte, or both. It is also understood that several different mechanisms operate to accomplish the same task: to provide the necessary nutrients within the egg for viable offspring. Three basic mechanisms are recognized during acquisition of these deutoplasmic components during oogenesis (terminology of SCHECHTMAN, 1955): (1) autosynthesis, whereby the oocyte itself produces yolk, (2) heterosynthesis, in which cells other than the oocyte produce yolk precursors, and (3) autoheterosynthesis ("mixed") which involves

Explanation of Figures 14 to 21

Figure 14: Vesiculation of the endoplasmic reticulum (arrow) is involved in proteid yolk formation. × 32 000

Figure 15: Endocytotic activity of the oolemma forms vesicles which contain an electron-dense particle (arrow) which is similar to granular material within the intercellular space (arrow). This material is PASM positive. × 26 600

Figure 16: Proteid yolk vesicles (V) increase in size by fusion of smaller proteid yolk vesicles and by fusion of ooplasmic vesicles. Note desmosome (arrow) between follicle cell and oocyte. × 10 200

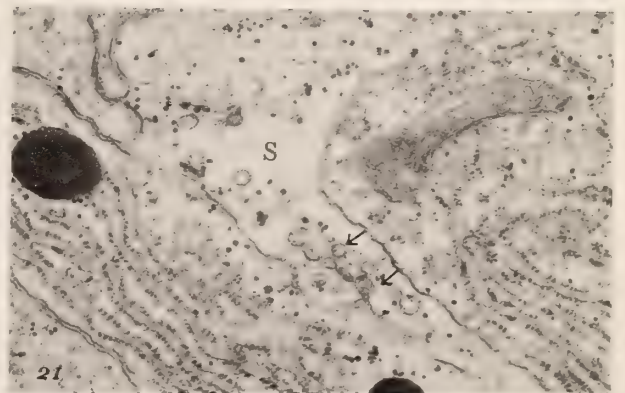
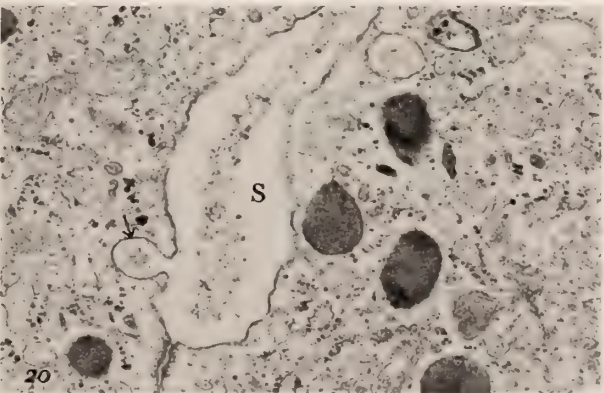
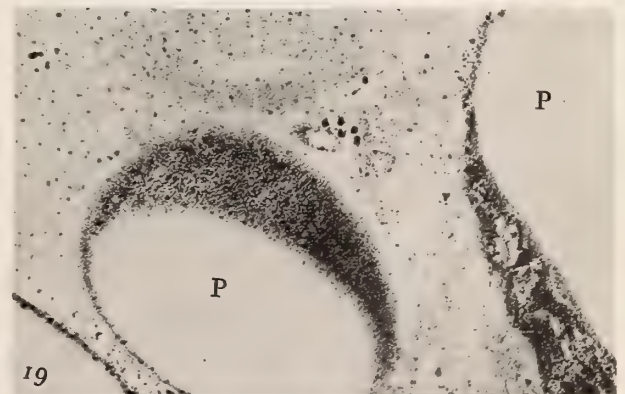
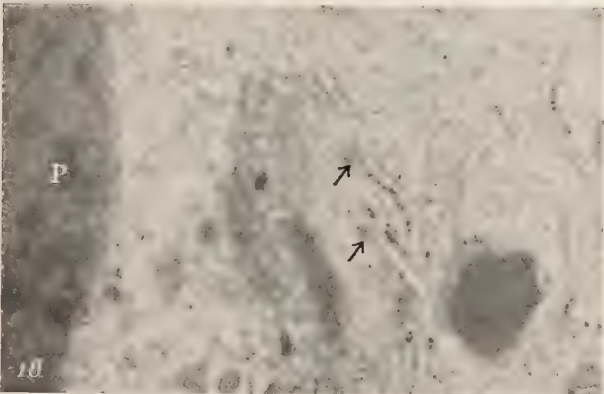
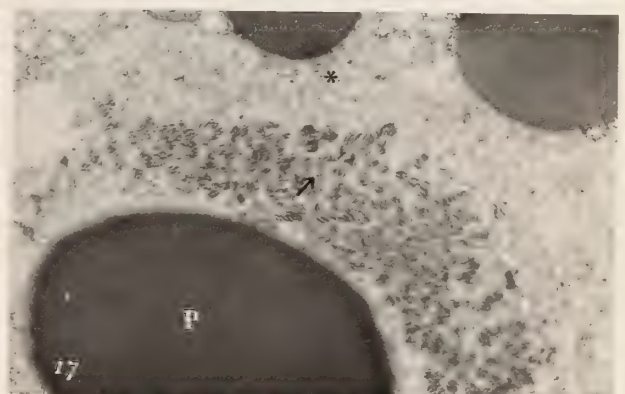
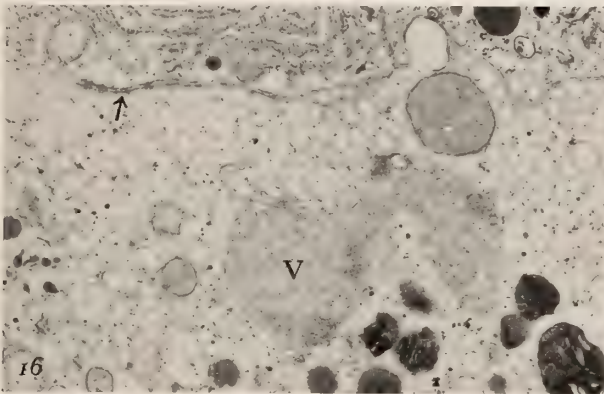
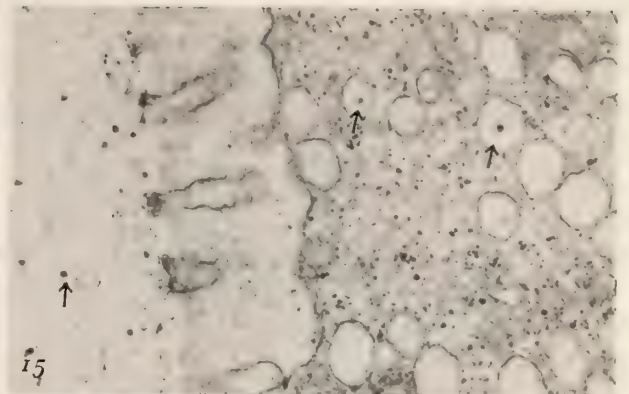
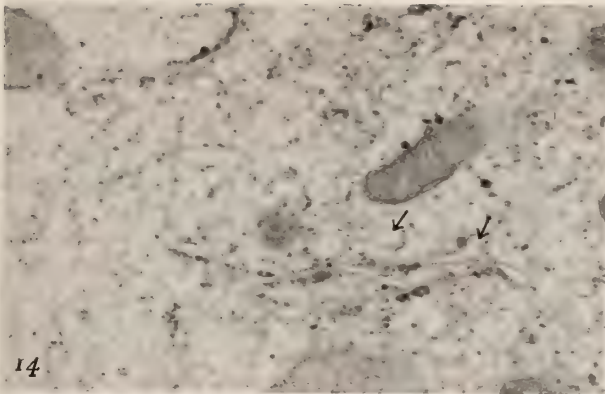
Figure 17: Condensation of material in proteid yolk vesicles (*) forms short fibrous material (arrow) which further condenses into the homogeneous proteid yolk platelet (P). × 20 500

Figure 18: Proteid yolk platelets (P) increase in size through fusion of ooplasmic vesicles and Golgi vesicles, in addition to proteid yolk vesicle fusion. The endoplasmic reticulum blebs small vesicles (arrow) which apparently fuse with the Golgi lamellae. × 50 000

Figure 19: Cortical region of proteid yolk platelets (P) react strongly to the periodic acid-silver methenamine technique indicating a carbohydrate moiety in this region. × 28 800

Figure 20: Follicle cells apparently release material into the intercellular spaces (S) by exocytosis (arrow). × 11 900

Figure 21: Follicle cells also release material into the intercellular spaces by blebbing (arrow) small flocculum filled vesicles. × 21 700



both the oocyte and cells other than the oocyte in yolk production. Autosynthetic yolk production seems to be common among the Spiralia, including Mollusca (HUEBNER & ANDERSON, 1976; ANDERSON, 1974; ECKELBARGER, 1980). Mixed yolk production is recognized in some fish, amphibians, annelids, crustaceans and numerous insects (ECKELBARGER, 1979, 1980). However, it is not common in molluscs (HUEBNER & ANDERSON, *op. cit.*; see, however, HILL & BOWEN, 1976). Although there is a wealth of information available on oocyte development, it has not been possible at present to organize a classification of vitellogenesis from an evolutionary point of view (ANDERSON, 1974; BOYER, 1972). Rather, it seems that the various mechanisms of vitellogenesis are more closely correlated with reproductive strategies and breeding behavior, at least in polychaetous annelids (ECKELBARGER, 1980).

Vitellogenesis in *Colus stimpsoni* appears to utilize both autosynthetic and autoheterosynthetic mechanisms. Autoheterosynthetic yolk production involves the follicle cells and the oocyte in production of the proteid (protein-carbohydrate) yolk platelets and, probably, glycogen. Lipoid yolk, on the other hand, appears autosynthetic. In proteid yolk formation, the sudden appearance of numerous vesicles in the ooplasm, concomitant with the presence of proteid yolk bodies, is interpreted as signalling the onset of this type of yolk formation. The origin of these vesicles appears to be the Golgi complex, vesiculation of the endoplasmic reticulum and through endocytotic activity of the oolemma. Endocytosis of extra-cellular material is indicated; however, when interpreting static electron micrographs, it is difficult to ascertain in which direction material may be moving. Undoubtedly some of the vesicles are involved in vitelline envelope production and are exocytotic in nature. Sequestering of extra-cellular material by the oocyte through endocytosis is recognized in a variety of animal groups (ECKELBARGER, 1979, 1980; DUMONT, 1969; HILL & BOWEN, 1976; HUEBNER & ANDERSON, 1976). This activity is generally indicated by formation of microvilli on the oolemma and/or a number of invaginations forming pits and vesicles subjacent to the oolemma. Also, the uptake of low molecular weight materials which are not rendered visible through electron microscopical techniques is very probable and has been suggested in yolk production and oocyte maintenance (NØRREVANG, 1965; ECKELBARGER, 1975; DONAHUE & STERN, 1968). Oocyte activities in proteid yolk formation in *C. stimpsoni* also involves the endoplasmic reticulum and the Golgi complex. This concert of endoplasmic reticulum and Golgi bodies in protein-carbohydrate yolk production is reported in a variety of molluscs (HUEBNER & ANDERSON, *op. cit.*; TAYLOR & ANDERSON, 1969; HILL & BOWEN, *op. cit.*;

BEAMS & SEKHON, 1966; ANDERSON, 1969; GÉRIN, 1976a, 1976b).

In *Colus stimpsoni*, proteid yolk formation is probably mixed (autoheterosynthetic) and involves yolk precursors synthesized by the oocyte as well as materials produced outside the egg. Mixed yolk formation in gastropods has been suggested in the slug *Agriolimax reticulatus* (Müller) (HILL & BOWEN, 1976) and also in the mud snail *Ilyanassa obsoleta* by TAYLOR & ANDERSON (1969). However, GÉRIN (1976a) made no mention of endocytotic activity in yolk formation in his study of vitellogenesis in *I. obsoleta*. In the freshwater pulmonate, *Biomphalaria glabrata*, however, follicle cells do not appear to be involved in vitellogenesis, but rather in the formulation of the follicular cavity (DE JONG-BRINK, *et al.*, 1976; see also for review of oogenesis in gastropods).

Glycogen also appears to be of mixed origin in *Colus stimpsoni*. Aggregates of α and β glycogen particles appear very early in oogenesis and increase in amounts throughout vitellogenesis. This early appearance of glycogen suggests an oocyte origin (also, see below in lipid yolk production). The extra-oocyte production of glycogen is indicated by the occurrence of intercellular glycogen particles which are apparently sequestered by the oocyte through endocytosis. Ooplasmic vesicles which contain a dense particle are indicative of this activity. These particles are a carbohydrate, indicated by the PASM technique and are very similar to β glycogen. Additional support for this hypothesis is the large aggregate of glycogen in the extra-cellular space around postvitellogenic oocytes. Presumably glycogen is released from the synthesizing cells and accumulates around postvitellogenic oocytes, since they no longer incorporate this material.

In *Colus stimpsoni* the oocyte stores vast amounts of glycogen and lipid, and these deutoplasmic components probably constitute the major form of nutritive supplies. The origin of lipid yolk is not clearly understood, since the majority of investigations reported in the literature deal with proteid yolk formation. In *C. stimpsoni*, lipid yolk production apparently involves both rough and smooth endoplasmic reticulum. Prolipoid bodies including their carbohydrate moiety, presumably glycogen, appear to be derived from the endoplasmic reticulum. The carbohydrate portion is parcelled out as the prolipoid yolk bodies fuse to form large droplets. This interpretation is suggested since the lipid yolk spheres do not appear to contain a carbohydrate, and glycogen particles are situated at the periphery of the lipid spheres (this association of lipid and glycogen is also noted by HILL & BOWEN, 1976, in *Agriolimax reticulatus* oocytes). Further, the enzymes associated with glycogen metabolism are known to be associated with smooth endoplasmic reticulum. Lipid yolk

synthesis by the endoplasmic reticulum is not without precedence. In a study of oogenesis in *Ilyanassa obsoleta*, GÉRIN (1976b) reported that the lipid droplets (lipochondria) are produced by the "yolk nucleus" (= "balbiani body"). This "yolk nucleus" is an array of concentric lamellae which GÉRIN (*op. cit.*) considered Golgi bodies. However, TAYLOR & ANDERSON (1969), in their study of oogenesis in *I. obsoleta*, considered this concentric array to be endoplasmic reticulum rather than Golgi lamellae, although they made no mention of lipid yolk formation. Comparing the electron micrographs of these two reports (GÉRIN, *op. cit.*; TAYLOR & ANDERSON, *op. cit.*), the interpretation of TAYLOR & ANDERSON (*op. cit.*) is more acceptable. Thus, lipid yolk production probably involves the endoplasmic reticulum in both *I. obsoleta* and *C. stimpsoni*.

Follicle Cells: Follicle cells are implicated in a variety of roles in oogenesis, ranging from influencing ooplasmic localizations, to structural support (HUEBNER & ANDERSON, 1976). The precise role(s) of follicle cells is not clearly known, and more emphasis should be given them in studies of oogenesis. In *Colus stimpsoni* follicle cells appear to play at least a synthetic role during vitellogenesis. These cells contain a well developed rough endoplasmic reticulum and Golgi complex which suggests high protein synthesizing capabilities and activities. The release of material by exocytosis and blebbing of the plasmalemma is indicated in electron micrographs. The occurrence of flocculent, granular and filamentous material and small, flocculum-filled vesicles in the extra-cellular spaces strongly suggests the release of material by the follicle cells for use by the oocyte. However, in the absence of experimental evidence, the precise nature of this material and the ultimate involvement of follicle cells in oogenesis cannot be ascertained from this study. From cytochemical evidence, however, it is suggested that the bulk of the material released by follicle cells is protein and carbohydrate in nature. These two components are probably sequestered by the oocyte and incorporated into proteid yolk platelets and/or stored as glycogen within the ooplasm during vitellogenesis.

Nutritive eggs: As indicated above, the major effort of the ovum in supplying nutriment for the embryo is accomplished during vitellogenesis. Additional food sources may also be supplied in the form of albumin which is placed in the spawn capsule for mechanical support of fertilized eggs and embryos and later consumed by the larvae. Many neogastropods add additional food sources through nutritive eggs (THORSON, 1935; RADWIN & CHAMBERLIN, 1973; LYONS & SPIGHT, 1973). These eggs are apparently normal zygotes but abort during various phases of development. In *Colus stimpsoni*, only a few eggs develop, 1 to 8, out of about 5 000 eggs deposited within a capsule; the remaining undeveloped eggs are consumed by the larvae (WEST, 1973). PORTMANN (1926, 1927, 1930) and HYMAN (1925) suggested that nutritive eggs are determined by fertilization with atypical (apyrene or oligopyrene) sperm. In *C. stimpsoni*, however, all sperm are apparently normal (WEST, 1978b). An alternative hypothesis is that eggs, like sperm, may also be atypical and give rise to nutritive eggs (BURGER & THORNTON, 1935). Evidence from the present study suggests that the oocytes in *C. stimpsoni* are normal in development, at least through vitellogenesis and germinal vesicle stages. RAVEN (1970) has implicated follicle cells in influencing ooplasmic localizations in *Lymnaea stagnalis*, and it is possible that such ooplasmic influence may be involved in nutritive egg determination; that is, certain oocytes may be determined to be nutritive eggs, or alternatively, to be viable ova, by certain interactions between the developing oocyte and follicle cells. However, this does not appear to be the case in *C. stimpsoni*. No unusual follicle cells or follicle cell-oocyte relationships were noted throughout this study. Within the range of histochemical techniques used in this study, no differences were noted in follicle cells or within oocytes, which further suggests that follicle cells are not obviously influencing oocyte determination. Because of the small percentage of viable embryos (< 0.1%), the bulk of oocytes appears nutritive in developmental commitment, and the probability of observing the small number of viable oocytes is low. For this reason, a large number of samples and animals were investigated; however, the possibility that these differences

Explanation of Figures 22 to 25

Figure 22: Glycogen particles (G) accumulate in the intercellular space around postvitellogenic oocytes (O). F - follicle cell.

× 11 900

Figure 23: Epon thick section of postvitellogenic oocyte. Lipoid (L) and proteid (P) yolk dominate the cytoplasm. The nucleolus (arrow) is eccentrically situated within a large acidophilic amphi-

nucleolus (*).

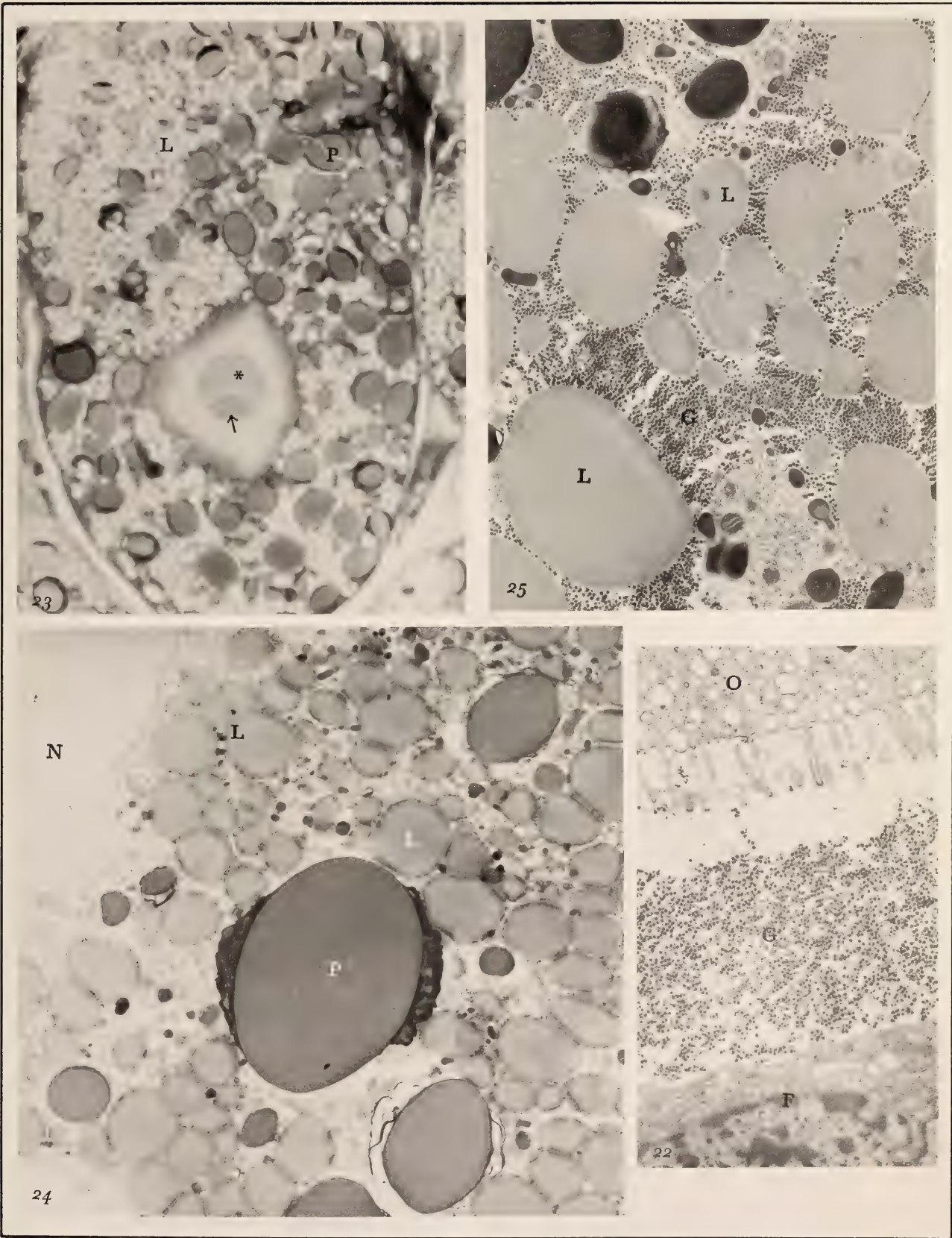
× 850

Figure 24: Postvitellogenic oocyte. N - nucleus; P - proteid yolk; L - lipid yolk

× 4 500

Figure 25: Aggregates of glycogen (G) occasionally occupy extensive ooplasmic areas in postvitellogenic oocytes. L - lipid yolk; P - proteid yolk

× 10 200



were not encountered must be borne in mind. It appears that other factors which are not visible through conventional electron microscopy are operating in nutritive egg determination, and investigations of early fertilization and embryology may be fruitful. The statement by BOYER that "... the nature of mosaicism will not be revealed by conventional methods of electron microscopy" is probably very true and applies equally well to the problem of the nutritive egg phenomenon.

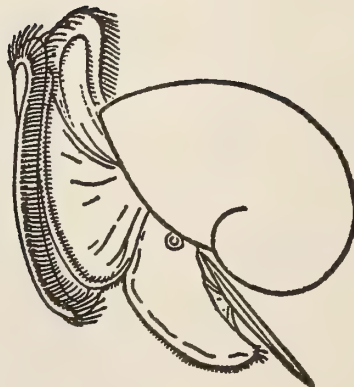
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Nominal Species of Living Oysters Proposed During the Last Fifty Years

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STUDYING BIOLOGICAL CLASSIFICATION and nomenclature is much like playing a game without beginning or end, in which the rules frequently change, and players of varying ability enter and leave as they please. Whether their actions are from the best or worst of motives, and whether they are ignorant of or choose to disregard the current rules, all players potentially influence subsequent events. Every player must be given the benefit of the doubt, for the most immutable and endurable rule of the game is, that it is not competitive but cooperative, in attempting to achieve an orderly arrangement of knowledge with unambiguous, if not stabilized, nomenclature. For some, this goal should also reflect as precisely as possible the phylogenetic history of organisms. Nowhere is the analogy of such a game more thoroughly exemplified than in the nomenclature of oysters.

Half a century ago LAMY (1929-1930) surveyed the living oysters and attempted to determine the biological species (which exist in nature as distinct entities) on the basis of the collection of the Natural History Museum of Paris. Numerous nominal species (named species, not necessarily valid as distinct biological ones) were also cited by him, which were not represented in the Paris museum. Of those he made no guess about their biological validity.

About 400 trivial names are included in the index of Lamy's paper. Some of the numerous homonyms he listed may be distinct biological species. But he even accepted as valid some pre-Linnaean names, specifically of Adanson, and post-Linnaean names of non-binomial authors such as Chemnitz, and names which had only been written on museum labels, such as those of Valenciennes and Jousseaume, but never published by them.

As might be expected, an impressive list of nominal genera in the Ostreidae had also accumulated by 1929. Lamy noted most of them in his introductory remarks, but he put all species of oysters in the genus *Ostrea* Linnaeus, 1758, a custom of many authors before and since, particularly when writing faunal catalogues. Since 1930 some

authors, chiefly those interested in the commercial production of oysters (e.g. THOMPSON, 1954), have put all living oysters in one of three genera: *Pycnodonte* Fischer de Waldheim, 1835 (often misspelled *Pycnodonta*: see STENZEL, 1971: N1105), *Ostrea* Linnaeus, 1758 and *Crassostrea* Sacco, 1897. RANSON (1960, 1967) advocated this system, and applied it most extensively. *Pycnodonte* was separated from the others because it has vesicular shell structure. The last two were separated from each other on the basis of the promyal passage on the right side of the excurrent mantle chamber being closed (*Ostrea*) or open (*Crassostrea*) (see STENZEL, 1971: N969); unfortunately, the condition of the promyal passage must be inferred for many species, since the anatomies of only a few have been studied. An additional basis for the three-genera system was used by Ranson. He made studies of the protoconchs (prodissoconchs), claiming he was able to recognize fundamental differences in the very ephemeral hinge dentition of the late larval and early post-larval shells, by which it is possible to separate not only genera, but all species of oysters from each other also. He did not describe any of these differences in words, and neither the photographs of the minute shells (RANSON, 1967) nor the line drawings (RANSON, 1960) allow other students to be certain which points he considered important in differentiating species. Whether these features have any validity I can not say, but they are certainly of little use in identifying post-larval oysters, many of which have lost their protoconchs through shell erosion. Even when the larval shell is present, it is usually impossible to determine its dentition, which is obliterated by later shell growth.

Using several additional shell characters, STENZEL (1971) proposed a more satisfactory classification of oysters. He divided the superfamily Ostreacea into four families (of which two fossil ones were dubiously included), five subfamilies (of which only three have living representatives), several tribes and 65 genera and subgenera.

His exhaustive study thoroughly reviewed the generic nomenclature. Of species, he dealt extensively only with those which are type-species. However, many other living species were dealt with incidentally, as examples of particular characteristics which he wished to discuss. He restricted *Pycnodonte* to species of fossil oysters, and introduced two new genera for the living species with vesicular shell structure: *Hyotissa* and *Neopycnodonte*. Because it is necessary to refer to Stenzel's classification in making generic allocations in the latter part of this paper, his classification of living oysters, with minor rearrangement and extension, is presented here. I have moved the Lophinae to a position between the Pycnodontinae and Ostreinae, and recognized as distinct the genera *Ostreola* and *Dendostrea* (which he synonymized with *Ostrea* and *Lopha*, respectively). My unpublished observations on the anatomy of those groups warrant these modifications.

Stenzel's Classification of Living Oysters.

OSTREACEA

GRYPHAEDAE

Pycnodontinae

Hyotissa Stenzel, 1971

Type: *Mytilus hyotis* Linnaeus, 1758 (OD)

Neopycnodonte Stenzel, 1971

Type: *Ostrea cochlear* Poli, 1795 (OD)

OSTREIDAE

Lophinae

Lopha Röding, 1798

Type: *Mytilus cristagalli* Linnaeus, 1758 (SD, Dall, 1898)

Dendostrea Swainson, 1853

Type: *Ostrea folium* Linnaeus, 1758 (SD, Herrmannsen, 1847)

Alectryonella Sacco, 1897

Type: *Ostrea plicatula* Gmelin, 1791 (OD)

Ostreinae

Ostreola Monterosato, 1884

Type: *Ostrea stentina* Payraudeau, 1826 (OD)

Ostrea Linnaeus, 1758

Type: *Ostrea edulis* Linnaeus, 1758 (SD, ICZN, Opin. 94)

Saccostrea Dollfus & Dautzenberg, 1920

Type: *Ostrea sacculus* Dujardin, 1835 (M)

(= *Ostrea cucullata* Born, 1778).

Striostrea Vyalov, 1936

Type: *Ostrea procellosa* "Valenciennes" Lamy, 1929 (OD)

(= *Ostrea margaritacea* Lamarck, 1819)

Crassostrea Sacco, 1897

Type: *Ostrea virginica* Gmelin, 1791 (OD)

Subfamily dubious

Anomiostrea Habe and Kosuge, 1966

Type: *Ostrea pyxidata* Adams and Reeve, 1842 (OD)

(not *O. pyxidata* Born, 1778 (Pectinidae) renamed

Anomiostrea coralliophila Habe, 1975)

During the fifty years since Lamy's paper was published, about one new trivial name per year has been proposed for living oysters. A few names appeared slightly before or at the time Lamy's paper went to press, which he could not include. These are listed below.

ORTON (1928) proposed 2 new genera (but did not adopt them himself) and 6 new trivial names for well known species, ostensibly to improve the nomenclature of oysters on the basis of making the literal meaning of the names more appropriate. His nominal taxa are not included in the list below because Lamy added a final paragraph to his paper, summarizing them, and IREDALE (1939) and STENZEL (1971) adequately disposed of Orton's names.

IREDALE (1939) named 7 new species of living oysters from Australia, poorly described but figured. RANSON (1967) added 8 nominal species from museum specimens, figuring only the protoconchs, and citing museum lots that represent them. In only one instance did he cite a lot as holotype (see *Ostrea rehderi*, below); another, *O. catalai*, is based on only a single museum lot. None of his species is described in words; even if his illustrations of the protoconchs are accepted as a "statement" about these species, they certainly do not differentiate them from other taxa, or sufficiently from each other, for the species to be recognized.

CATALOGUE OF SPECIES

In the following catalogue, the trivial names are alphabetically arranged, with author and year of publication indicated for each. The name as originally introduced is presented, showing the genus in which it was placed, or the kind of subspecific taxon in the case of a few, introduced at that level. The source of publication is given, with notation of illustrations, if any, and the type locality.

Where possible, I have attempted to allocate the trivial taxon to its proper genus, as understood in the outline of genera above. I am very grateful to Thomas R. Calnan for making it possible for me to see several of the papers cited.

1. *amasa* Iredale, 1939.

Saxostrea amasa Iredale, 1939. Sci. Repts. Brit. Mus. Great Barrier Reef Expedit. 1928-29, Moll., p. 399, Pl. 7, fig. 8. Type Loc., Caloundra (Queensland), Australia. THOMPSON (1954) accepts this species as valid, noting that it is probably what LAMY (1929) called *Ostrea forskali* var. *mordax* Gould. Iredale's species is possibly a *Saccostrea*.

2. *arbicola* Dautzenberg, 1929.

Ostrea inaequalis Sowerby, 1871 var. *arbicola* Dautzenberg, 1929. Moll. Test. Mar. de Madagascar, p. 554-555. Not figured. Type Loc., not stated, evidently Madagascar. The generic allocation of this trivial name, proposed as a "variety," depends on what oyster Dautzenberg identified as *O. inaequalis* Sowerby, 1871; this is uncertain, but from the habitat (adhering to mangrove roots) and the geographic source of his material, this is possibly a *Saccostrea*.

3. *ariakensis* "Fujita" Wakija, 1930.

Ostrea ariakensis "Fujita" Wakija, 1930. Fourth Pacific Science Congress (Batavia, Java) Proc. 3:345-347. Not figured. Listed as a reference, thus: "*O. ariakensis* (Wakija M.S.) Fujita, Nihon Suisan Dobutsugaku, 1913, p. 519." This may mean that Fujita proposed the name in 1913, based on a manuscript of Wakija, but I have been unable to locate any such reference. An extensive description in the 1930 reference notes it is very similar to *O. gigas* (which is a *Crassostrea*). Type Loc., "Along the western coast of Korea, probably extending to the coasts of China, and in Japan it is only found in the Bay of Ariake and the Bay of Shiranuhi on the northeastern coast of Kyushu". KURODA & HASE (1952) do not cite the species, but the name is accepted as a valid species by Ranson (1967) and by Kira (1962).

4. *awajiensis* "Hirase" Hatai, 1930.

Ostrea edulis awajiensis n. subsp. "Hirase" Hatai, 1930. Fourth Pacific Science Congr. (Batavia, Java) Proc. 3:223. No description or illustration. For the species, the parenthetical synonym is given: "*O. denselamellosa* Lischke." The subspecific trivial name is essentially nude (see also *O. japonica* "Hirase" HATAI, 1930).

5. *bartschi* Ranson, 1967.

Ostrea bartschi Ranson, 1967. Revue des Travaux de l'Inst. Pêches Maritimes 31(3):243-244, fig. 40, p. 243 (two very poor photographs of exterior of left and right valves of protoconch, and drawing of interior of left valve protoconch). No description. Fifteen lots are cited from four museums, but none are designated type. Localities are the Philippines, Siam, and various islands of the East Indies. The species is unrecognizable from the original publication.

6. *benefica* Bartsch, 1945.

Ostrea benefica Bartsch, 1945. Smithsonian Misc. Colls. 104(16):1-2, pls. 1, 2. Type Loc., Sandakan, British North Borneo. This is a large *Crassostrea*, probably only an environmental variant of *C. gigas* (Thunberg, 1793).

7. *bresia* Iredale, 1939.

Ostrea bresia Iredale, 1939. Sci. Repts. Brit. Mus. Great Barrier Reef Expedit., 1928-29, Moll., p. 396-397, pl. 7, fig. 4. Type Loc., Seaforth, north of Mackay, Queensland, Australia. Although STENZEL (1971) accepts Thompson's (1954) view that this is only an ecomorph of *Lopha cristagalli* Linnaeus, 1758, I think it is more likely to belong to the genus *Alectryonella* as defined by Stenzel.

8. *caparti* Ranson, 1967.

Crassostrea caparti Ranson, 1967. Revue des Travaux de l'Inst. des Pêches Maritimes 31(2):199, fig. 25, p. 199 (three poor photographs of the protoconch). No description. No citation of type or type locality. Only two localities are listed, Siam and Timor, each lot in a separate museum. The species is unrecognizable from his account.

9. *catalai* Ranson, 1967.

Ostrea catalai Ranson, 1967. Revue des Travaux de l'Inst. des Pêches Maritimes 31(3):246, fig. 43; p. 246 (line drawings of exterior of protoconch of right valve). No description. Only one lot is cited from the Muséum d'Histoire Naturelle of Paris (evidently not numbered); it is from Nouméa, New Caledonia, which is therefore the type locality. The published data are too insufficient for species recognition.

10. *charlottae* Finlay, 1928.

"*Ostrea charlottae* n. sp. (sic) for *O. hyotis* Sutter, 1913, Man. N.Z. Moll., p. 889, pl. 57, fig. 2; not of Linne." Finlay, 1928, New Zealand Institute Trans., 59:265-266, pl. 40, figs. 25-26. Type Loc., Queen Charlotte Sound,

New Zealand. From Finlay's figure, this is close to or identical with *Ostrea angasi* Sowerby, 1871.

11. *commercialis* Iredale and Roughley, 1933.

Ostrea commercialis Iredale and Roughley, 1933. Linn. Soc. New So. Wales, Proc., 58:278. Not figured. Proposed as a replacement name for oysters of New South Wales, Australia, previously identified under six trivial names (of species of other regions). A brief description is given, but no precise type locality cited (evidently New South Wales, Australia). This is probably a member of the genus *Saccostrea*, as STENZEL (1971) noted.

12. *complanata* Fenaux, 1944.

Ostrea complanata Fenaux, 1944. Inst. Océanographique (Monaco) Bull. No. 861, p. 1, pl. 1, figs. 1-2. Poorly described in Latin and French. No measurements are given, nor type locality cited, which is evidently the Mediterranean Sea. The figure indicates it is in the genus *Crassostrea*.

13. *coralliophila* Habe, 1975.

Anomiostrea coralliophila Habe, 1975. Venus (Japanese Jour. Malacol) 33:184. Substitute name for *Ostrea pyxidata* Adams and Reeve, 1848, not Born, 1778 (Pectinidae).

14. *corteziensis* Hertlein, 1951.

Ostrea corteziensis Hertlein, 1951. So. Calif. Acad. Sci. Bull., 50:68, pl. 24, figs. 1-2. Type Loc., Kino Bay, Sonora, Mexico, Gulf of California. This is a *Crassostrea*.

15. *dactylena* Iredale, 1939.

Ostrea commercialis dactylena "ecomorph nov." Iredale, 1939. Sci. Repts. Brit. Mus. Great Barrier Reef Expedit. 1928-29, Moll., p. 399, pl. 7, fig. 6. Type Loc. Lindeman Island (Queensland?), Australia. Probably a *Saccostrea*.

16. *elongata* Grabau and King, 1928.

Ostrea chemnitzii Hanley, var. *elongata* Grabau and King, 1928. Shells of Peitaiho, p. 58, 164. Not figured. Type Loc., not specified, evidently Peitaiho, China. Not *Ostrea elongata* Born, 1778 (Pectinidae).

17. *futamiensis* Seki, 1929.

Ostrea futamiensis Seki, 1929. Imperial Acad. Japan Proc., 5:477, figs. 1-9, p. 479. Type Loc., Futami, Hyogo Prefecture, Japan. This is probably an *Ostreola*.

18. *gradiva* Iredale, 1939.

Saxostrea gradiva Iredale, 1939. Sci. Rept. Brit. Mus. Great Barrier Reef Expedit. 1928-29, Moll., p. 400, pl. 7, fig. 10, 10a, 10b. Type Loc., on a mangrove root, Low Isles (Queensland, Australia). This is possibly a *Striostrea*, but THOMPSON (1954:152) considered it a synonym of "*Crassostrea echinata* (Quoy and Gaimard, 1835)" which, if true, would place Iredale's species in *Saccostrea*.

19. *guyanensis* Ranson, 1967.

Crassostrea guyanensis Ranson, 1967. Revue des Travaux de l'Inst. des Pêches Maritimes 31(2):169-170, fig. 15, p. 169 (drawing of exterior view of protoconch of left valve). No description. No type or type locality was cited, but 38 lots are listed, from 10 museums. All localities are from French Guiana, Surinam, Trinidad and Brazil. The species is unrecognizable from the original publication.

20. *hefferdi* Finlay, 1928.

Ostrea hefferdi Finlay, 1928. New Zealand Inst. Trans., 59:265, for the New Zealand form of *Ostrea tatei* Sutter, 1913. Sutter's species had as type a specimen from Eocene strata of Australia, although he thought it also occurred living in New Zealand. A neotype was selected by Finlay from Dunedin Harbor, which is therefore the type locality.

21. *hiranoi* Baker and Spicer, 1930

Ostrea hiranoi Baker and Spicer, 1930. San Diego Soc. Nat. Hist., Trans. 6(6):173, pl. 18, figs. 1-3. Type Loc., sixty fathoms depth, about five miles off the Bay of Obama on the northern coast of Hondo, Japan. This is *Neopycnodonte cochlear* (Poli, 1795).

22. *iredalei* Faustino, 1932.

Ostrea iredalei Faustino, 1932. Philippine Jour. Sci. 49(4):546-547, pl. 1, figs. 1-4. Type Loc., Navotas, Malabon, Parañaque, and other places in Manila Bay. This is a *Crassostrea*, possibly *C. gigas* (Thunberg, 1793).

23. *irregularis* "Tokunaga" Grabau and King, 1928.

Ostrea irregularis "Tokunaga" Grabau and King, 1928. Shells of Peitaiho, p. 58, 163. Not figured; Type Loc. not specified, evidently Peitaiho, China. The brief description is insufficient to allow generic allocation.

24. *japonica* "Hirase" Hatai, 1930.

Ostrea edulis japonica "Hirase" Hatai, 1930. Fourth Pacific Science Congress (Batavia, Java, 1969) Proc.

3:223. No description, figure or type locality; a parenthetical synonym is indicated, "*O. denselamellosa* Lischke)." The name is nude, and seems not to have been used in later literature on the oysters of Japan.

25. *kauaia* Dall, Bartsch and Rehder, 1938.

Ostrea kauaia Dall, Bartsch and Rehder, 1938. Bernice P. Bishop Mus. Bull., 153:112-113, pl. 30, figs. 8-9. Type Loc., U.S. Bur. Fisheries Steamer Albatross at Station 4132, near Kauai (Hawaiian Ids.) in 257-312 fathoms on fine gray sand and mud bottom.

26. *kupua* Dall, Bartsch and Rehder, 1938.

Ostrea kupua Dall, Bartsch and Rehder, 1938. Bernice P. Bishop Mus. Bull., 153:111, pl. 30, figs. 1-4. Type Loc., Pearl Harbor, Oahu, Hawaii. This is probably a *Dendostrea*.

27. *laterostrata* Fenaux, 1942.

Ostrea (Ostreola) laterostrata Fenaux, 1942. Inst. Oceanogr. (Monaco) Bull., No. 861, p. 1, text fig. Type Loc., not specified, evidently from the Mediterranean coast of France. The Latin and French descriptions are poor, with no measurements given. I think, from the figure, the specimen is *Neopycnodonte cochlear* (Poli, 1795), and that the author has misconstrued the concept of *Ostreola*.

28. *laysana* Dall, Bartsch and Rehder, 1938.

Ostrea laysana Dall, Bartsch and Rehder, 1938. Bernice P. Bishop Mus. Bull. 153:111, pl. 32, figs. 5-8. Type Loc., U.S. Bur. Fisheries Steamer Albatross at Sta. 3854, off Laysan Island (Hawaiian Ids.) in 30-20 fathoms on white sand, pebbly and rocky bottom. This is *Neopycnodonte cochlear* (Poli, 1795).

29. *malabonensis* Faustino, 1932.

Ostrea malabonensis Faustino, 1932. Philippine Jour. Sci. 49(4):547, pl. 2, figs. 3-5. Type Loc., Malabon, Rizal, Philippines. This is possibly an *Ostreola*.

30. *nippona* Seki, 1934.

Ostrea nippona Seki, 1934. Venus, Japanese Jour. Malacol. 4(5):276-279. Text figs. 1-4, p. 277 and 6-15, p. 278. Type Loc. Harima (Japan). Possibly an *Ostrea* s.s.

31. *nomades* Iredale 1939.

Ostrea nomades Iredale, 1939. Sci. Repts. Brit. Mus. Great Barrier Reef Expedit., 1928-29, Moll., p. 395, pl. 7, figs. 1, 1a, 1b. Type Loc., not specified, although

"typical specimens" are cited from Stradbroke Island, Queensland, Australia, and fig. 1a of pl. 7 is from "North-West Islet, Capricorn Group, Queensland." This is probably an *Ostreola*.

32. *procles* Iredale, 1939.

Ostrea procles Iredale, 1939. Sci. Repts. Brit. Mus. Great Barrier Reef Expedit., 1928-29, Moll., p. 396, pl. 7, fig. 2. Type Loc., "under coral blocks at Low Isles, Michaelmas Cay (Queensland, Australia)." This is probably *Hyotissa numisma* (Lamarck, 1819).

33. *quirites* Iredale, 1939.

Ostrea quirites Iredale, 1939. Sci. Repts. Brit. Mus. Great Barrier Reef Expedit., 1928-29, Moll., p. 396, pl. 7, fig. 3. Type Loc. "dredged in Port Curtis in about 9 fathoms (Queensland, Australia)."

34. *rehderi* Ranson, 1967.

Ostrea rehderi Ranson, 1967. Revue des Travaux de l'Inst. Pêches Maritimes 31(3):244, fig. 41; p. 244 (three poor photographs of protoconch). No description. Only three lots are cited, all from the Philippines, all at the U.S. Natl. Mus. Nat. Hist. One lot is designated type of the species, USNM 235745. "Philippines, off Jolo, Jolo Id., USBF Sta. 5145." The species is unrecognizable from the original publication.

35. *respondens* Dautzenberg, 1932.

Ostrea (Lopha) Förskali Chemnitz, 1785 var. *respondens* Dautzenberg, 1932. Jour. de Conchyl. 76:87. New name for "*cornucopiae* auct. (non Chemnitz)." This name resulted from LAMY's (1929) decision that the oysters which would today be called *Saccostrea cucullata* (Born, 1778) should be given different names when they occur in the eastern Atlantic from those which occur in the Indo-west Pacific.

36. *sedea* Iredale, 1939.

Ostrea sedea Iredale, 1939. Sci. Repts. Brit. Mus. Great Barrier Reef., Moll., p. 397, pl. 7, fig. 5. Type Loc., not specified. The figured specimen is "from under stones at Lindeman Island, Whitsunday Group," Queensland, Australia, but Michaelmas Cay, Low Isles, is also cited.

37. *setoensis* Habe, 1957.

Ostrea sedea setoensis subsp. nov. Habe, 1957. Venus, Japanese Jour. Malacol. 19:180-181. Not figured. Type Loc., Seto, Shirahama, Wakayama Prefecture, Honshu, Japan. Probably an *Ostreola*.

38. *sikamea* "Amemiya" Hatai, 1930.

Ostrea gigas Thunberg var. *sikamea* var. nov. "Amemiya" Hatai, 1930. Fourth Pacific Science Congress (Batavia, Java, 1929) Proc. 3:223. No description or illustration. A nude name, apparently never published by Amemiya.

39. *syriaca* Pallary, 1938.

Ostrea (Ostreola) stentina Payraudeau var. *syriaca* Pallary, 1938. Jour. de Conchyl. 82:48, pl. 2, figs. 15-16. Type Loc., "De Jounieh à Alexandrette et Payas" (Eastern Mediterranean, north of Beirut).

40. *thaanumi* Dall, Bartsch and Rehder, 1938.

Ostrea thaanumi Dall, Bartsch and Rehder, 1938. Bernice P. Bishop Mus. Bull. 153:114-115, pl. 32, figs. 1-4. Type Loc., Mokuoloe Island, Kaneohe Bay, Oahu, Hawaii. This is *Hyotissa numisma* (Lamarck, 1819).

41. *thomasi* McLean, 1941.

Ostrea (Ostrea) thomasi McLean, 1941. Notulae Naturae (Acad. Nat. Sci. Philadelphia) No. 67, p. 7, pl. 3, figs. 1-2; pl. 4, figs. 1-2. Type Loc., Off Palm Beach, Florida, in 300 feet of water. This is an *Hyotissa*. *Ostrea thomasi* "Conrad" Cope, 1867 (Acad. Nat. Sci. Phila., Proc. 1867, p. 139) is a nude name which does not invalidate McLean's species.

42. *tridacnaeformis* Ranson, 1967.

Crassostrea tridacnaeformis Ranson, 1967. Revue des Travaux de l'Inst. des Pêches Maritimes 31(2):198-199, fig. 24, p. 198 (drawings of interior and exterior views of protoconchs of both valves). No description. No citation of type or type locality, although only six lots are cited, from two museums. The localities listed are Red Sea and New Caledonia. The species is unrecognizable from the original publication.

43. *valettei* Ranson, 1967.

Ostrea valettei Ranson, 1967. Revue des Travaux de l'Inst. des Pêches Maritimes 31(3):217-218, fig. 29; p. 217 (line drawing of protoconch). No description. No type or type locality cited, although 24 lots, from five museums are listed, all from the coast of Brazil, Uruguay and Argentina. The species is unrecognizable from the original publication.

44. *weberi* Olsson, 1951.

Ostrea weberi Olsson, 1951. Nautilus 65:6-7, pl. 1, figs.

1-4. Type Loc., Key West, Florida. This is possibly a *Striostrea*.

45. *winckworthi* Ranson, 1967.

Ostrea winckworthi Ranson, 1967. Revue des Travaux de l'Inst. des Pêches Maritimes 31(3):245-246, fig. 42; p. 245 (three poor photographs of the protoconch). No description. No designation of type or of type locality. Twelve museum lots are cited, from seven museums. Localities include Japan, China, Northern Australia, Andaman Islands and Ceylon. The species is unrecognizable from the original publication.

POSTSCRIPT

I am indebted to Dr. John W. Tunnell, Jr., for calling my attention to the following new name, which appeared after this paper was in press:

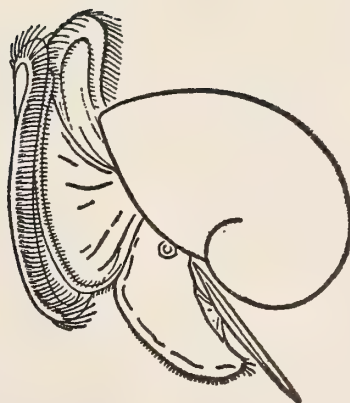
46. *paraibanensis* Singarajah, 1980.

Crassostrea paraibanensis Singarajah, 1980. Bull. of Marine Science 30(4):837-846; fig. 2, p. 836; fig. 3, p. 837; fig. 5, p. 843. Type Loc., Salinas and Livramento, Paraiba River estuary . . . northern part of Brazil. This is correctly placed generically.

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Helminthoglypta reederi spec. nov.

(Gastropoda: Pulmonata: Helminthoglyptidae)

from Baja California, Mexico

BY

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(1 Plate; 1 Text figure)

THE LAND SNAIL GENUS *Helminthoglypta* Ancey, 1887, is almost exclusively Californian. At the northern limit of the range of the genus, *Helminthoglypta hertleini* Hanna and Smith, 1937, and *H. arrosa mailliardi* Pilsbry, 1927, extend into the southernmost part of Oregon. At the southern limit of the range, *H. tudiculata* (Binney, 1843) and several subspecies of *H. traski* (Newcomb, 1861) extend along the coast to the vicinity of Santo Tomas, San Vicente, and, reportedly, San Antonio del Mar, near Colonet, in the Estado de Baja California, Mexico.

In November 1973, my graduate students Carl C. Christensen and Richard L. Reeder and I, accompanied by my long-standing friend and companion, James B. Cartwright, undertook to investigate the malacofauna of the region of Baja California inland from Colonet and San Telmo as far east as the crest of the Sierra San Pedro Martir. A relatively good road to the astronomical observatory at an elevation of about 2 750 m (9 000 ft.) greatly facilitated our travel.

The most common large snails of the coastal region of that part of Baja California, namely in the vicinity of Colonet, San Telmo, and Colonia Guerrero, are *Plesarionta stearnsiana* (Gabb, 1867) and *Xerarionta levis* (Pfeiffer, 1845).

PILSBRY (1939) described *Plesarionta*, *Xerarionta*, and *Eremarionta* as subgenera of *Micrarionta* on the basis of major differences in anatomy and shell morphology. BEQUAERT & MILLER, (1973: 106) raised *Eremarionta* to generic rank on the basis that shell morphologies and reproductive anatomies were significantly different from *Micrarionta* s.s. to render questionable the implied close phylogeny conferred by subgeneric status. For the same reason, *Plesarionta* and *Xerarionta* are here raised to generic rank.

At lower elevations, wherever rock outcrops or talus accumulations afforded adequate cover, we found shells of the ubiquitous *Plesarionta stearnsiana* as expected. We did not, however, find any shells of *Xerarionta levis*. This species apparently does not venture far from the shore line.

At the higher elevations, in pines and white firs, we were unable to find any large snails at all until we reached an extensive rock pile at an elevation of about 2 575 m (8 450 ft.) which eventually yielded, after much arduous digging, a large, new species of *Helminthoglypta*, described below.

Only two live adults were obtained, and the shells were so thin and fragile that one of them was subsequently broken. The granitic, acid-humus soil caused rapid disintegration of empty shells so that good shells were very rare.

A subsequent trip to the region, in July 1980, failed to yield any live animals, and two days of extensive digging by five of us in nearby rockslides rewarded us only with six worn adult shells.

Helminthoglypta reederi W. B. Miller, spec. nov.

Diagnosis: A large sized, globose *Helminthoglypta* with thin shell and moderately densely papillose sculpture.

Description of Shell of Holotype: Shell large, thin, low-conic, helicoid, umbilicate, the umbilicus one-tenth of the shell diameter. Color light golden-brown with darker, chestnut-brown band on the shoulder, bordered above and below by a narrow band lighter in color than the body of the shell. Embryonic shell of $1\frac{3}{4}$ whorls, very finely, closely, wrinkly-granulose, superimposed with a few, widely-spaced papillae. Post-embryonic whorls with

coarser, radial growth wrinkles superimposed by closely-spaced, raised papillae arranged in parallel gradually-descending spiral rows and persisting to the peristome and to the base of the body whorl. On the body whorl and penultimate whorl, a few scattered, faint, spiral grooves can be detected occasionally near the suture. Periostracum glossy, with satiny sheen. Last part of body whorl descends abruptly to the ample, oblique aperture. Peristome slightly reflected, more so at the umbilicus. Diameter 27.2 mm, height 17.0 mm, diameter of umbilicus 2.7 mm; number of whorls $5\frac{1}{4}$.

Reproductive System Anatomy: The reproductive system is typical for the genus, with a large dart sac at the end of a capacious atrial sac and two mucus glands, each with a large mucus bulb; the ducts from the mucus bulbs join into a single duct before entering the atrial sac just below the dart sac. The long spermathecal duct leads to a capacious, spherical spermatheca, and bears a long spermathecal diverticulum. The penis and epiphallus form a long, continuous duct; at its proximal end, the epiphallus bears a long epiphallic caecum, and at its distal end, it consists of a tube within a tube, capable of partial eversion into the penial chamber; there is no verge. The vas deferens passes around the dart apparatus, and the penial retractor muscle is inserted on the epiphallus.

Type Locality: Baja California, Mexico. Sierra San Pedro Martir, in rock outcrops in a small canyon which crosses the road to the astronomical observatory, at a distance of about 2.5 road km (1.5 miles) below the observatory housing area; elevation ca. 2575 m (8450 ft.). Collected 3 November 1973 by W. B. Miller, R. L. Reeder, and C. C. Christensen.

(adjacent column →)

Figure 1

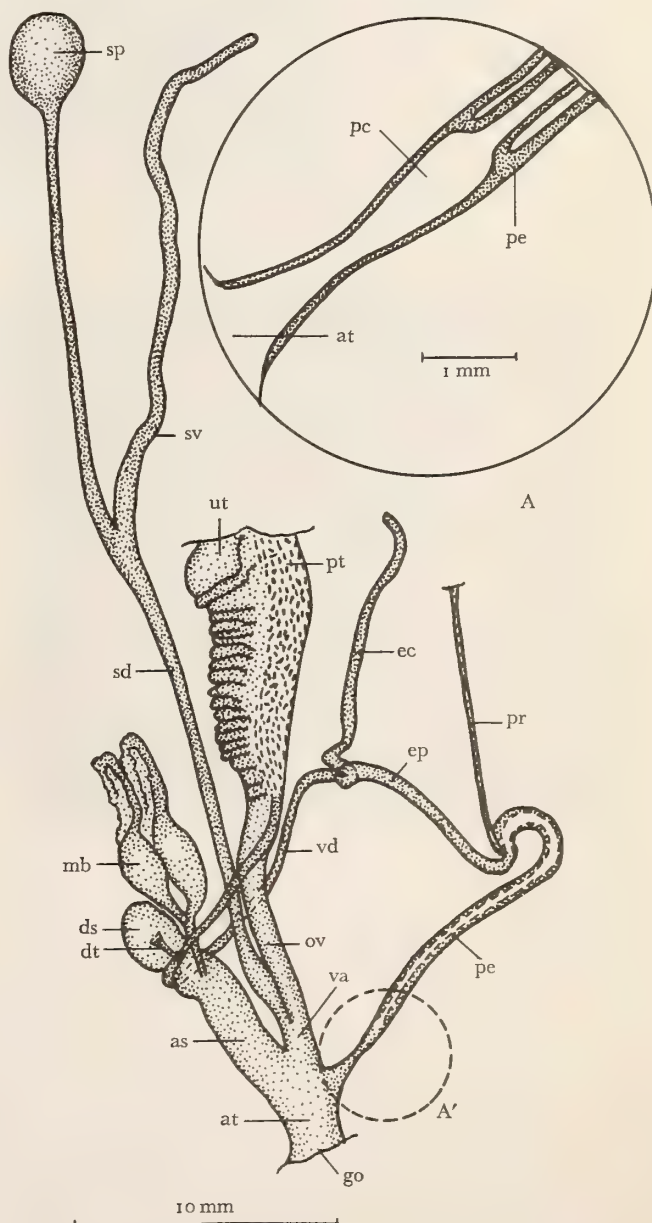
Helminthoglypta reederi W. B. Miller, spec. nov.

Distal reproductive structures of holotype; drawing made from projection of stained whole mount. Distal portion of penis A' magnified in inset A to show details in sagittal section.

as - atrial sac; at - atrium; ds - dart sac; dt - dart;
ec - epiphallic caecum; ep - epiphallus; go - genital orifice;
mb - mucus bulb; ov - oviduct; pc - penial chamber;
pe - penis; pr - penial retractor; pt - prostate;
sd - spermathecal duct; sp - spermatheca;
sv - spermathecal diverticulum; ut - uterus; va - vagina;
vd - vas deferens

Type Material: Holotype: California Academy of Sciences no. 019732; Paratypes: U.S. National Museum no. 784636; R. L. Reeder collection no. 405; W. B. Miller collection no. 6319.

Discussion: The reproductive system anatomy of the genus *Helminthoglypta* is not diagnostically useful at the species level. At the species-group level, it can be used to differentiate only between a few major groups. PILSBRY



(1939: 170) erred in establishing the subgenus *Charodotes*, 1939, on the basis of the apparent absence of a double tube within the penis-epiphallus complex, because repeated investigations by the author and by W. O. Gregg of *H. traski* (Newcomb, 1861) and many of its subspecies, as well as *H. petricola* (Berry, 1916) and its subspecies have always revealed the presence of the double tube structure. ROTH (1973) reported that *H. t. fieldi* Pilsbry, 1930, possesses a thick-walled inner tube within the distal portion of the penis and accordingly raised it to full specific status. Evidently, the species assigned to *Charodotes* bear no significant anatomical differences from those of *Helminthoglypta sensu stricto*, and *Charodotes* therefore cannot be considered a valid subgenus.

By its anatomy, *Helminthoglypta reederi* clearly belongs to the group of *H. traski* and *H. petricola*. By its shell characteristics, it shows affinities with *H. petricola* particularly with the more papillose subspecies *H. p. sangabrielis* (Berry, 1920) and *H. p. zechae* (Pilsbry, 1916). *H. reederi* is distinguished by the dense papillation on all of its whorls and by the almost complete absence of spiral grooves. Of the six adult paratypes collected in 1980, only four were entire shells. Their measurements varied only slightly from those of the holotype, with the shell heights ranging from 16.5 mm to 17.3 mm and the maximum diameters from 26.5 mm to 29.0 mm. All of the shells were papillose and three had faint, spiral grooves near the suture on the body whorl while the other three had no grooves at all.

Geographically, its nearest relatives are *Helminthoglypta traski* from Santo Tomas and *H. t. misiona* Chace, 1937, from La Mision Valley, both of which are characterized by numerous, often prominent, spiral grooves and by the almost complete absence of papillae on the body whorl. *Helminthoglypta tudiculata* has been reported from Punta Banda and from the vicinity of San Antonio del Mar (PILSBRY, 1939: 71) along the coast, but its heavily mal-leated shell sets it apart from any other *Helminthoglypta* in Baja California.

Distribution and Habitat: *Helminthoglypta reederi* shells have been found in rockslides and rock piles at the base of granite cliffs and outcrops for about one mile

upward along the small canyon that opens at the Observatory road at the type locality; elevations ranged from 2575 to 2625 m (8450 to 8600 ft.). A small stream runs along the bottom of the canyon, bordered by numerous clumps of monkey flowers (*Mimulus guttatus* and *M. cardinalis*) and columbine (*Aquilegia formosa*). On the north-facing slope of the canyon, there are large white firs (*Abies concolor*) and Jeffrey pines (*Pinus jeffreyi*) and an understory of *Philadelphus microphyllus* and *Quercus chrysolepis*.

Living *Helminthoglypta reederi* probably live deep in fissures of the granite cliffs and outcrops. In addition to *H. reederi*, we found many specimens of *Vallonia cyclophorella* Sterki, 1892, and *Pupilla hebes* (Ancey, 1881) and a few specimens of *Euconolus fulvus* (Müller, 1774).

Etymology: This species is named after Richard L. Reeder, friend and colleague, whose discovery of a shell fragment, after the rest of us had given up, led to renewed efforts and ultimate discovery of two live adults deep within the rock pile.

ACKNOWLEDGMENTS

I wish to express my gratitude to my former graduate students and friends Noorullah Babrakzai, Carl C. Christensen, H. Lee Fairbanks, and Richard L. Reeder and to my long-standing old friend and tutor in natural history James B. Cartwright for their assistance and camaraderie in collecting the scarce paratypes. I also want to thank Barry Roth for reading and criticizing this manuscript.

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Explanation of Figures 2, 3 and 4

Helminthoglypta reederi W. B. Miller, spec. nov.

Shell of Holotype, CAS no. 19732; diameter 27.2 mm

Figure 2: Apertural View

Figure 3: Apical View

Figure 4: Umbilical View



Figure 2



Figure 3



Figure 4

Correct Authorship and Date Citations for Several Californian Opisthobranch Gastropod Taxa Described in Publications by Cooper and Cockerell

BY

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WITHIN THE PAST 10 YEARS, numerous technical and popular reference books have been published which identify or index various opisthobranch mollusks from the Pacific coast of America (e.g., RUSSELL, 1971; KEEN, 1971; ABBOTT, 1974; SMITH & CARLTON, 1975; ALLEN, 1976; STRAUGHAN & KLINK, 1980; BEHRENS, 1980; and MORRIS, ABBOTT & HADERLIE, 1980). These important works are widely distributed and are used by numerous researchers, students, and others as primary taxonomic sources. However, a close scrutiny of the opisthobranch sections of these books reveals significant discrepancies in authorship and publication dates among those species described in papers written by James Graham Cooper and Theodore Dru Alison Cockerell. Since 22 of these species account for nearly 15% of the currently recognized opisthobranch taxa from the Oregonian and Californian zoogeographic faunal provinces, a proper resolution of these differences may be useful.

Table 1 lists the complete and correct citations (including original page of description) for 31 specific and 4 generic taxa. The arrangement of the first 22 species follows BEHRENS (1980) and CADIEN (in STRAUGHAN & KLINK, 1980). Those 9 species marked with an * are either junior synonyms or are considered questionable or unrecognizable by modern workers.

DISCUSSION

Cooper published 3 articles in 1863 in which he described opisthobranch taxa. The species described in the first paper (COOPER, 1863a) have often been cited erroneously as Cooper, 1862. This article appeared in the Proceedings of the California Academy of Natural Sciences for 1862, but its date of publication was January 1863, as printed on page 205 of the issue (see also FERREIRA & BERTSCH, 1975: 327).

The other Cooper articles usually have appeared correctly in bibliographic and taxonomic references.

COCKERELL (1901a) described 2 eolid and 1 dolid nudibranch species in the Journal of Malacology. This date usually has been cited correctly. Cockerell submitted a description of 3 species of chromodorids from southern California for publication in The Nautilus. This paper was published in June 1902, nearly 7 months after the publication of his article (in the 28 November 1901 issue of the British journal Nature) on the pigments of these same 3 nudibranchs. Nomenclatural priority clearly belongs to this paper in Nature (COCKERELL, 1901b) because it includes (recognizable) descriptions with proper scientific names. Such an inadvertent publication of new taxa prior to the intended description is reminiscent of the circumstances leading to *Murex hirasei* Hirase, 1915 (cf. RADWIN & D'ATTILIO, 1976: 66). The proper citation for the three species (original genus given for simplicity) *Chromodoris universitatis*, *C. porterae*, and *C. macfarlandi* is Cockerell, 1901.

Taxa described in COCKERELL & ELIOT, 1905, have received the greatest amount of inconsistent references. Reading the text carefully can eliminate these problems. All new taxa in this work require listing as "... in Cockerell & Eliot, 1905." On page 31, Eliot writes, "The new specific names are due to him, [i.e., Cockerell] the generic names to me." Throughout the text (with the exception mentioned below) new taxa are indicated solely by "n. sp." Further indication is unnecessary since Eliot's statement unequivocally designates authorship. It should be noted that modern authors rightly prefer to state authorship with the introduction of each new specific name (cf. FARMER in FARMER & SLOAN, 1964, and BERTSCH in BERTSCH, FERREIRA, FARMER & HAYES, 1973).

The genus *Dirona* and the species *D. picta* and *D. albo-lineata* are clearly and properly attributed to MacFarland, since the authors do not use just manuscript names, but actually present complete quotations from the notebooks of MacFarland describing these taxa. Cockerell & Eliot inserted these quotations as separate entities, not as auxiliary or supportive quotes of another author for their work. This is tantamount to including a section or chapter writ-

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ten by MacFarland. Therefore, just as it is correct to cite LANCE in KEEN, 1971, and McDONALD in SMITH & CARLTON, 1975, for the proper authorship of the respective nudibranch sections in those works, the proper citation for *Dirona*, *D. albolineata* and *D. picta* is MACFARLAND in COCKERELL & ELIOT, 1905.

The abbreviation for authorship of taxa described in Cockerell & Eliot, 1905, is either Cockerell, 1905, Eliot, 1905 (*Phyllobranchopsis*), or MacFarland, 1905. The complete, correct citation, however, is preferable because it is clearer and facilitates bibliographic information retrieval.

ACKNOWLEDGMENTS

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Table 1

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Aplysiopsis enteromorphae (Cockerell in Cockerell & Eliot, 1905: 52-53)
Acanthodoris rhodoceras Cockerell in Cockerell & Eliot, 1905: 38-39
Aldisa sanguinea (Cooper, 1863a: 204)
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Dendrodoris nigromaculata (Cockerell in Cockerell & Eliot 1905: 40-41)
Diaulula sandiegensis (Cooper, 1863a: 204-205)
Doriopsisilla albopunctata (Cooper, 1863c: 58)
Mexichromis porterae (Cockerell, 1901b: 79)
Trapania velox (Cockerell, 1901a: 87)
Triopha catalinae (Cooper, 1863c: 59)
Dendronotus iris Cooper, 1863c: 59
Antiopella barbarensis (Cooper, 1863c: 59-60)
Armina californica (Cooper, 1863a: 203-204)
Dirona albolineata MacFarland in Cockerell & Eliot, 1905: 46
Dirona picta MacFarland in Cockerell & Eliot, 1905: 46-48
Coryphella cooperi Cockerell, 1901a: 85-86
Facelina stearnsi Cockerell, 1901a: 86
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Dirona MacFarland in Cockerell & Eliot, 1905: 45-46
Phyllobranchopsis Eliot in Cockerell & Eliot, 1905: 52
Strategus Cooper, 1863a: 202
Navarchus Cooper, 1863b: 8
* *Doris alabastrina* Cooper, 1863a: 204
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* *Janolus coeruleopictus* Cockerell in Cockerell & Eliot, 1905: 48-50
* *Aeolis opalescens* Cooper, 1863a: 205
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Influence of Terminal End of Burrow on Callum Shape in the Rock Boring Clam *Penitella penita* (Conrad, 1837)

(Bivalvia : Pholadidae)

BY

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(3 Plates)

IN THE MONTEREY BAY REGION of California the rock boring pholad *Penitella penita* is a common inhabitant of sedimentary rock in the intertidal zone near Santa Cruz. It also lives in subtidal shale in the southern part of Monterey Bay but in far fewer numbers (HADERLIE, 1980).

Like other members of the pholad subfamilies Mar-
tensiinae and Jouannetiinae, *Penitella penita* has a deter-
minate type of growth which is unusual in molluscs
(EVANS, 1968c). After larval settlement and initial pene-
tration of the substrate, the animal grows as it bores deeper
into the rock. During this active growing and boring period
P. penita remains sexually immature, and the shell gapes
widely anteriorly exposing the powerful, sucker-like foot.
When it reaches adult size after about 3 years (when the
shell averages 55 mm long), the animal undergoes meta-
morphosis. At this time the foot atrophies, the adductor
muscles shrink, the gonads develop, a siphonoplax is
formed, and the pedal gape is closed by a heavy hemi-
spherical callum consisting of two parts with a narrow
slit between halves. The slit is covered by a periostracum.
When complete, the callum extends dorsally covering the
umbonal reflection, and encloses the anterior muscle by
doubling upon itself (TURNER, 1954, 1955). The entire
anterior end of the animal thus becomes quite hemispher-
ical. After metamorphosis no significant growth occurs and
the animal ceases to lengthen the burrow. It becomes sex-
ually mature soon after metamorphosis and may live for
many years until external erosion of the burrow exposes
the animal to predation.

In studies over the past several years designed to mon-
itor growth rates of various pholads and mytilids using
radiographic techniques, I have removed a variety of im-
mature bivalve borers from their natural rock habitats
and introduced them into "artificial" burrows drilled into
stone panels. These panels, of a variety of sedimentary
stone and of differing hardness, were then replaced in the
intertidal zone in the sea and recovered bimonthly for
x-ray analysis in an attempt to detect growth of the ani-

mals and deepening of the burrows. The results of these
long-term studies will be published later. This present
short report deals with observations made on several occa-
sions where, following metamorphosis, the callum and
entire anterior end of the shell valves of *Penitella penita*
were of an odd shape clearly reflecting the shape of the
blind end of the artificial burrow.

In pioneering studies on growth rates of *Penitella penita*
in sedimentary rocks in the intertidal zone on the Oregon
coast, EVANS (1968a, 1968b, 1968c) found that animals
introduced into artificial burrows he had drilled into the
native rock often assumed the shape of the burrow. Under
natural conditions, *P. penita* forms a pear-shaped conical
burrow with a rounded terminal end and a small opening
on the surface for extension of the siphons. Most individ-
uals when mature are swollen and fit very snugly in the
burrow (see Figure 2). EVANS (1968b) reported that im-
mature animals introduced into artificial cylindrical bur-
rows tended to become cylindrical adult clams with an-
terior ends that mirrored the ends of the drilled holes. He
suggested that at metamorphosis the mantle was appar-
ently extended so as to fill the space available to it.

My more recent observations on this same species con-
firm and extend those of Evans. Many immature speci-
mens of *Penitella penita* have been removed from shale of
the Monterey Formation from the intertidal zone at Santa
Cruz. These animals, still in the active boring stage, were
then introduced into artificial burrows drilled into the
edges of sawn panels of shale. The size of the hole was such
that the animal fitted into it quite snugly. The open end
of the burrow was then plugged with a cork perforated
with a 6 mm opening to allow for extension of the siphons.
The drill bit used created a cylindrical hole with a flat
bottom, in the very center of which was a small conical
depression made by the central spur on the drill bit (see
Figure 1).

Removing, without injury, small, delicate pholads from
their natural burrows is difficult and many of the ex-

tracted animals transplanted to artificial burrows did not survive. Those that did survive either adapted to the new environment and began to grow and excavate a deeper burrow, or they remained quiescent for a time then metamorphosed and formed a callum which reflected in great detail the shape of the blind end of the burrow.

Figure 1 shows the shape of a typical drilled artificial burrow with the perforated stopper in place. Figure 2 illustrates a stone panel split open to show the burrow and a living, metamorphosed specimen of *Penitella penita* (seen from left side). At the time the specimen shown in the photograph was introduced into the burrow as an immature form on 20 April 1978 the burrow was 52 mm deep and 15 mm in diameter and the animal had a shell length of 25 mm and a maximum diameter of 14 mm. At the termination 9 months later on 22 January 1979, when the panel was split and the photograph taken, the burrow was 75 mm deep and 23 mm in diameter and the animal had a shell length of 50 mm and a maximum diameter of 23 mm. This specimen had not only survived the transplantation but had grown and increased the size of the burrow before reaching adult size and undergoing metamorphosis. The shape of the shell is fairly typical of mature animals found in natural burrows in shale.

Figure 3 illustrates an animal that did not grow or excavate after being transplanted to a similar artificial burrow. This animal underwent metamorphosis soon after being transplanted (as determined by x-ray analysis), and formed a callum that followed closely the contours of the blind end of the burrow including the depression left by the central spur on the drill bit. When transplanted, the immature animal had a shell length of 35 mm and a diameter of 19 mm. The burrow had a depth of 64 mm and a diameter of 19 mm. When exposed on 22 January 1979, 9 months later, the animal had an overall shell length of 45 mm and a diameter of 19 mm. The size of the burrow was the same as at the beginning. The animal had not increased the size of the burrow and had not grown in diameter. The increase in shell length was due primarily to the addition of the odd-shaped callum.

Figure 4 is an enlarged lateral view of the left valve of a specimen similar in size and shape to that shown in place in Figure 3. This clearly shows the inflated parts of the callum and the general cylindrical shape of the shell. Figure 5 is a dorsal view of the same animal, and Figure 6 is an anterior view showing the periostracum-covered slit in the callum and the position of the central protuberance, limited to the left part of the callum.

Explanation of Figures 1 and 2

Figure 1: Experimental block of Monterey Shale split open to show shape of artificial burrow (64 mm deep; 19 mm diameter) created by drill bit. Note shape of blind end of burrow including central depression left by spur on drill. Perforated cork (at right) closes the burrow.

Figure 2: Experimental block of Monterey Shale split open to show an adult *Penitella penita* in place in an artificial burrow. Animal had been in the burrow for 9 months, had grown, and had enlarged the burrow before metamorphosing and forming a typical hemispherical callum.

Explanation of Figures 3 and 4

Figure 3: Experimental block of Monterey Shale split open to show an adult *Penitella penita* in place in an artificial burrow. This animal had not grown nor increased size of burrow, but had metamorphosed and formed a callum that reflected the shape of the terminal end of the burrow. Animal was still alive after 9 months in the burrow and siphons extended out of perforation in cork at right.

Left valve was cracked in opening the burrow.

Figure 4: Left valve of *Penitella penita* from artificial burrow showing the atypical shape of the callum which matched the contours of the terminal end of the burrow. Overall shape of the shell valves are more cylindrical than in a typical specimen from a natural burrow.

Explanation of Figures 5 and 6

Figure 5: Dorsal view of same specimen as shown in Figure 4. Note inflated region of callum which extends up over the umbos and the atypical flaring of the posterior end of the shell near the siphonoplax.

Figure 6: View of anterior end of same specimen as shown in Figure 4, dorsal side at top. Note protuberance on left half of callum (right center in photograph).

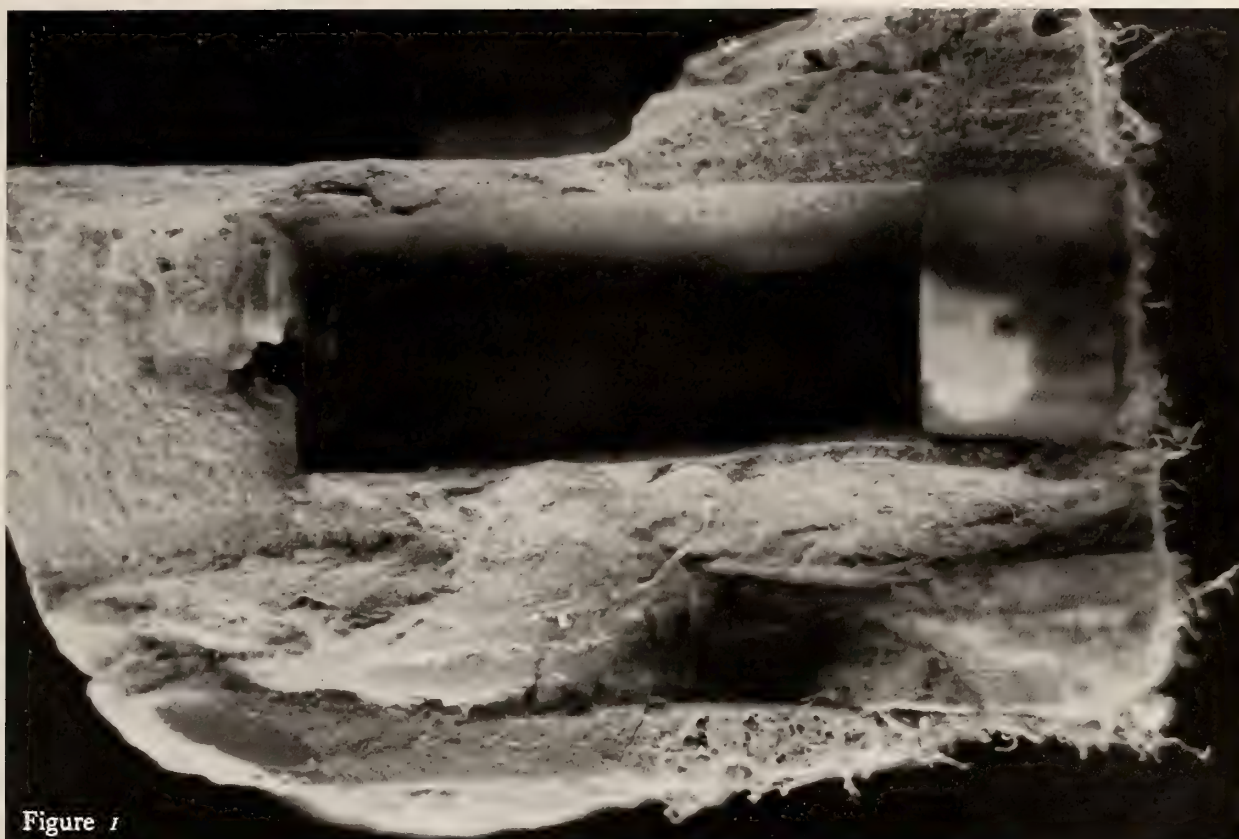


Figure 1

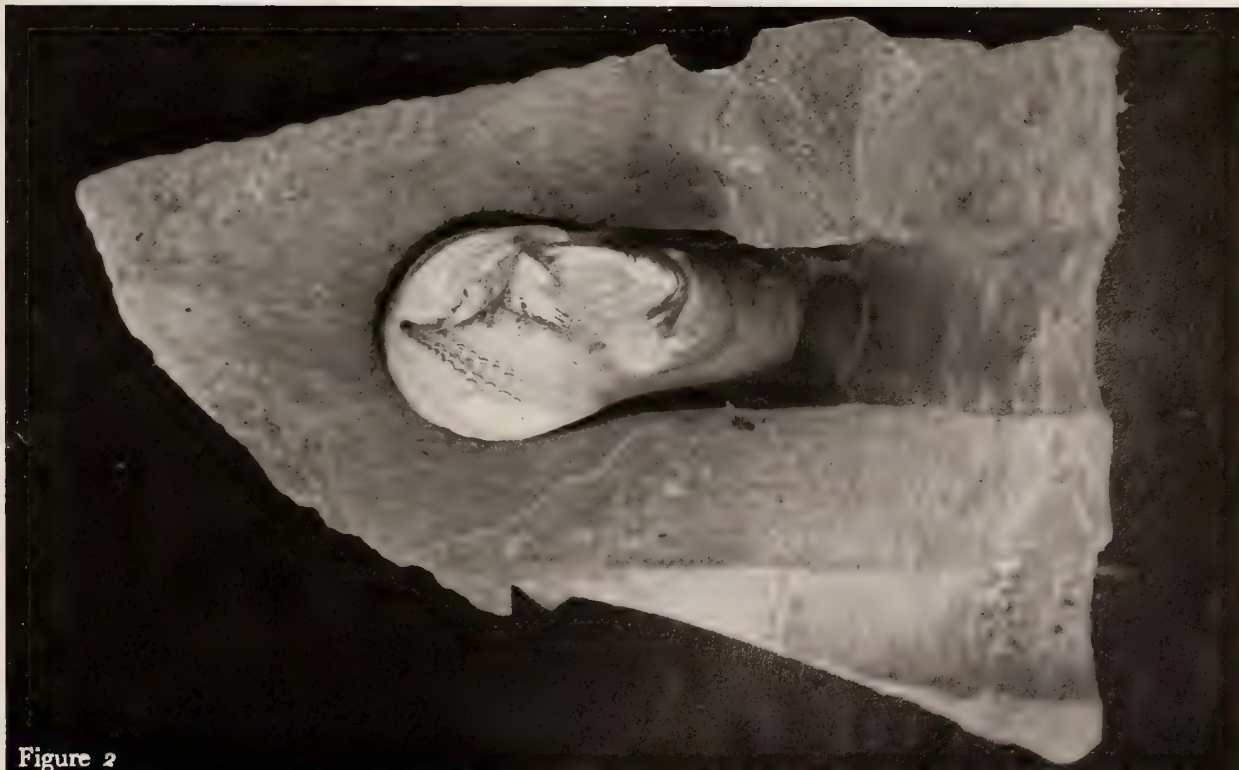


Figure 2

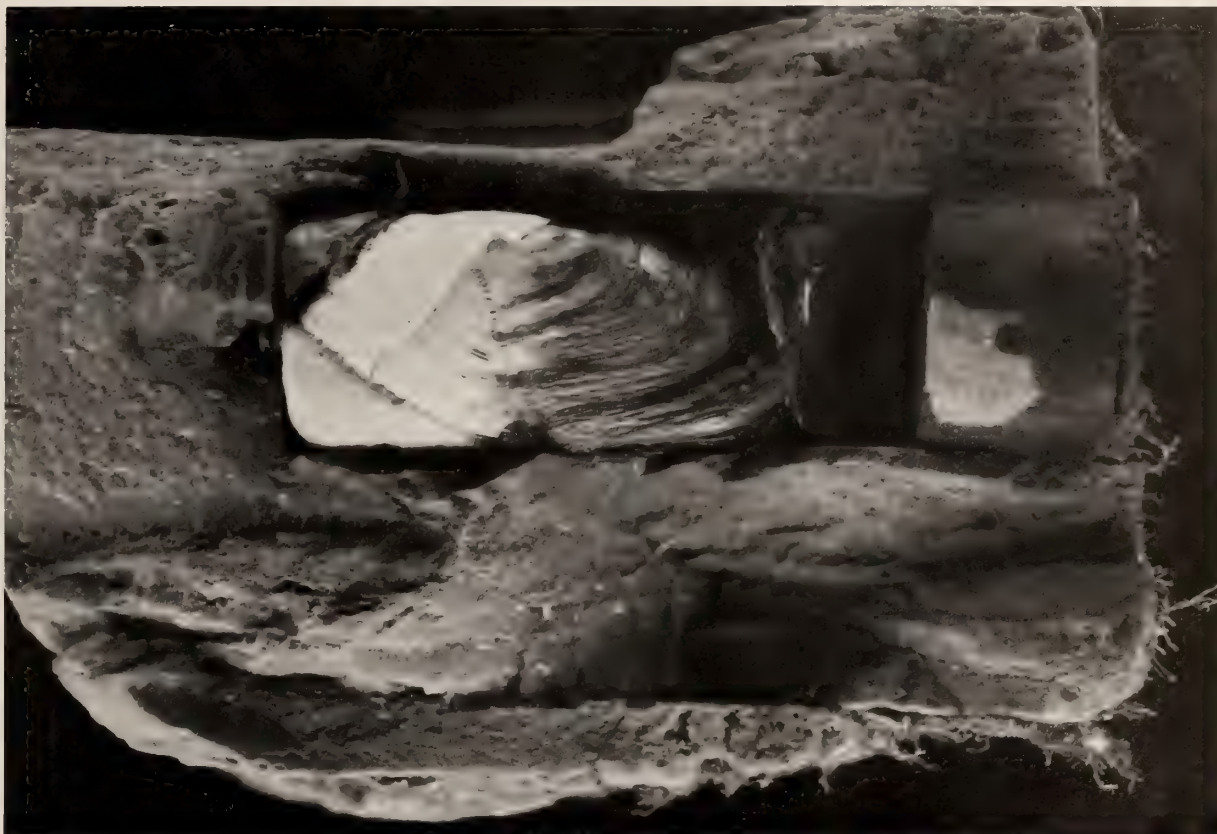


Figure 3

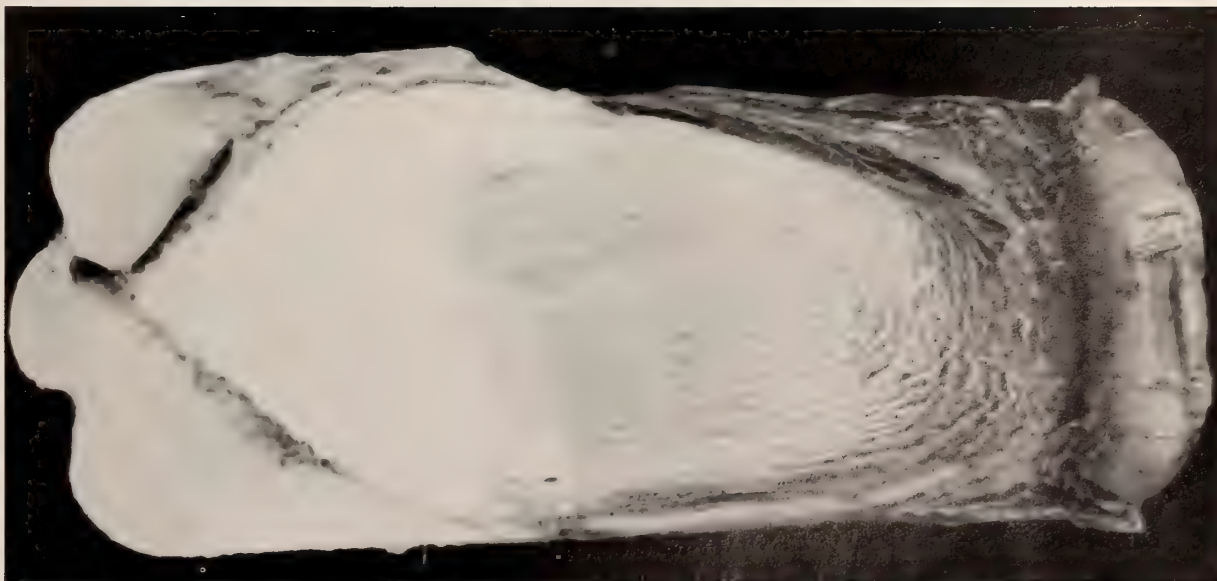


Figure 4



Figure 5

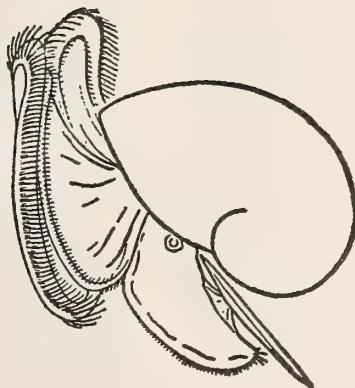


Figure 6

It is apparent that *Penitella penita* uses the shape of the terminal end of the burrow as a mold on which the mantle lays down the callum during metamorphosis.

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A Possible Mechanoreceptor Associated with the Anterior Byssus Retractor Muscle of *Mytilus edulis* Linnaeus

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(2 Text figures)

INTRODUCTION

MECHANICALLY SENSITIVE receptor units have been found in the anterior byssus retractor muscle (ABRM) of *Mytilus edulis* Linnaeus, 1758 by LACOURSE & NORTHROP (1978). They speculated that the receptors responsible for the electrophysiological sensory activity within the ABRM may be the same putative receptors described morphologically by GILLOTEAUX (1971, 1972), in the ABRM of *M. edulis* as "neuromuscular associations." These associations, stained by an osmium-zinc iodine technique, were interpreted by GILLOTEAUX (1971, 1972) as interoreceptors. Analogous associations have been observed by LACOURSE *et al.* (1979) in the ABRM of *M. edulis* using the method of cobalt chloride axonal iontophoresis, an intracellular staining technique. Using this technique they also established a direct morphological route between the associations and the pedal ganglion via the visceral nerves and the cerebropedal nerve.

In the present study we were able to observe with good morphological detail these associations.

METHODS AND MATERIALS

Specimens of adult mussels were collected at Ocean Beach, New London, Connecticut, and held in tanks of cooled, aerated sea water in the laboratory until use.

The right or left ABRM was dissected from the animal and the clinging connective tissue. It was then placed into a bath of cold filtered sea water. The muscle was then transferred into a 1% solution of pure methylene blue chloride and shredded by hand into smaller slender pieces with fine glass probes. Following the method of ZAWARZIN (1912) the tissue was put in the stain in such a way that parts of the shredded muscle tissue were exposed to the air. Within 5-30 minutes the associations were observable.

RESULTS AND DISCUSSION

The association is composed of one efferent nerve branch supplying the nerve ending. The nerve fiber, 0.5-1.1 μm in diameter, forms a large spiral, twisted around the smooth muscle fiber. The muscle fiber of the association is modified; it is thinner, 3.6-4.05 μm in diameter, than the contractile well-shaped normal fiber, 4.0-4.5 μm in diameter. Just before the nerve terminates in the muscle fiber, it swells forming a bipolar unit which has a length of 3.5-4.1 μm and a width of 0.75-1.8 μm . Not well shown in this photo-micrograph (Figure 1), but illustrated in Figure 2, are very thin processes extending from the bipolar unit.

It is our speculation that the bipolar unit is the sensory cell's soma and the thin processes from the soma are its dendritic tree. Similar bipolar cells have been observed embedded in connective tissue around the shafts of thick

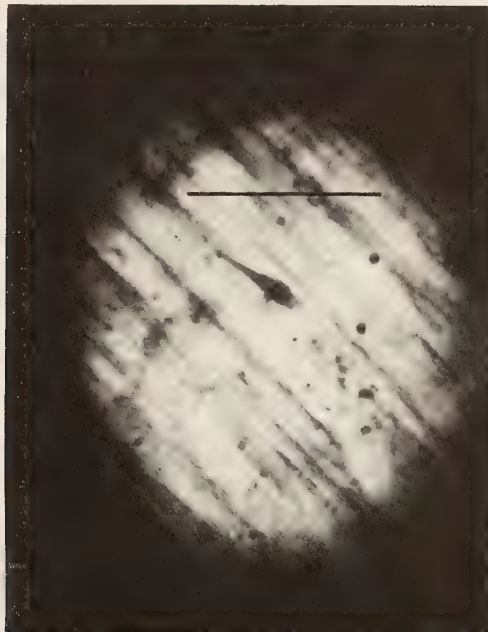


Figure 1

A neuromuscular association in the ABRM of *Mytilus*
photomicrograph of the mechanoreceptor, 8 μ m rule

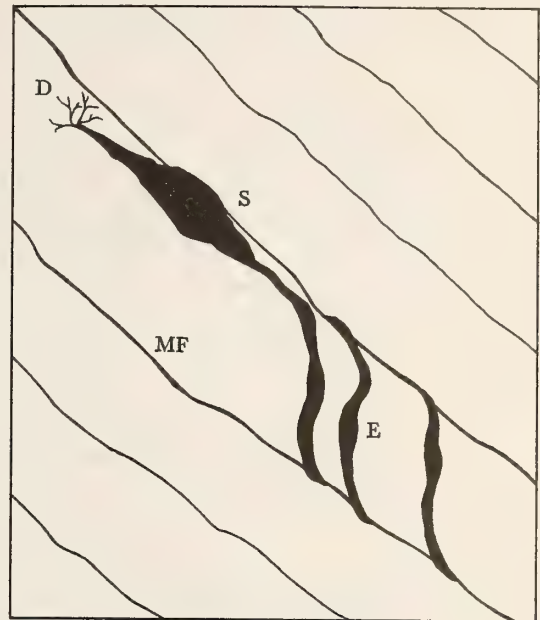


Figure 2

Illustration of the mechanoreceptor

D – dendritic tree S – soma E – efferent axon
MF – modified muscle fiber

apodemes of the tailspine muscle of *Limulus polyphemus* by EAGLES & HARTMAN (1975), who speculated that these bipolar cells are tension receptors.

Our observations and previously-reported findings suggest that these neuromuscular associations are the mechanoreceptors described electrophysiologically by LACOURSE & NORTHROP (1978). The probable mechanoreceptor is composed of a modified muscle fiber and a sensory nerve.

ACKNOWLEDGMENTS

We should like to thank the University of Connecticut Research Foundation (Grant 0505-35-184) for their partial support of this research. We should also like to thank Dr. J. Gilloteaux for his personal communications.

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Spawning Cycle and Fecundity
in a Population of *Petricola pholadiformis*
(Pelecypoda : Petricolidae)
from Milford, Connecticut

BY

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(2 Plates; 2 Text figures)

INTRODUCTION

THE FALSE ANGEL WING, *Petricola pholadiformis* Lamarck (1818), is a highly-specialized pelecypod that frequently inhabits peat and hard clay substrates. Except for two major works on its functional morphology (PURCHON, 1955; ANSELL, 1970), and another describing its natural history (DUVAL, 1963), only scattered references to the species' distribution appear in the literature (SIKES, 1910; CONNELL, 1955; JOCQUE & VANDAMME, 1971; MORRIS & ROLLINS, 1977). However, there has been little work done on its reproductive biology.

Petricola pholadiformis is a dioecious pelecypod, the sexes of which are distinguishable only after examination of the gonads. COE (1943) includes *P. pholadiformis* in his study of the origin and early development of the gonad of pelecypod molluscs through sexual differentiation. However, he does not include a discussion of gametogenic development in this species. Similarly, DUVAL (1963) reports the frequency and duration of spawning for a number of populations of *P. pholadiformis* along the southeast coast of Britain without providing any specific information on the gametogenic cycle itself.

In an effort to clarify the reproductive biology of *Petricola pholadiformis* this study was designed to 1) define and categorize the sequence of gametogenic development based on microscopic examination of gonadal tissue, 2) determine the frequency and duration of the spawning cycle in a natural setting and 3) estimate the total number of eggs produced by females of different sizes. This investigation represents the only account of the reproduc-

tive ecology of a North American population of this species.

MATERIALS AND METHOD

Specimens of *Petricola pholadiformis* were collected from a small population located at the westernmost section of Silver Beach of Long Island Sound in Milford, Connecticut, USA (41°12'N; 73°05'W). They were found in the intertidal zone, burrowed in deposits of mud and peat on the site of a relict *Spartina alterniflora* marsh. Clams were collected once a month from March, 1979 through May, 1980 and twice a month during February and April, 1980. Sample sizes varied from 15 to 40 clams, 11.8-62.1 mm shell length. A total of 492 clams were examined of which only one was immature. The remaining 491 mature clams were used in the analysis of the reproductive cycle.

The clams were returned to the laboratory where they were numbered and their maximum length (± 0.1 mm) determined. The visceral mass, excluding the foot and mantle, was removed, fixed in 10% buffered formalin (HUMASON, 1967) and its displacement volume taken to determine its size. The tissues were then prepared for histological examination (BROUSSEAU, 1978). A microscopic examination was made to assign each individual to the appropriate category of gonadal condition. There was no evidence of seasonal changes in gonadal color as reported by DUVAL (1963).

The number of oocytes present in each female gonad was determined in the following manner. Using an ocular grid, triplicate counts were made of the number of oocytes

present per 0.47 mm^2 of gonad for each of 65 females reported in a "ripe" condition (when virtually all the oocytes were fully grown). All oocytes were counted, including those cells in which no nucleus was visible. This area was then multiplied by the mean oocyte diameter ($45 \mu\text{m}$) in order to determine oocyte densities on a cubic basis. An estimate of the total number of oocytes in the gonad could then be calculated on the basis of gonad size.

The relationship between the size of the "ripe" female gonads and the volume of the total visceral mass was determined as follows: Entire Viscera from 15 "ripe" females ($33.3\text{--}58.2 \text{ mm}$ shell length) were sectioned at $12 \mu\text{m}$. Next, 5 sections from each individual were chosen using a random numbers table, mounted in a 35 mm slide projector and the projected tissue outlines were traced. A planimeter was used to estimate the percentage of gonad tissue present. A correction factor representing the proportion of gonad in the total visceral mass was used in estimating the total number of oocytes per individual (0.63 ± 0.074 at 95% C.I.).

Photomicrographs of representative stages of the male and female reproductive cycle were taken with a Zeiss light microscope at 125X magnification using a 35 mm camera. Panatomic X ASA32 film was used.

RESULTS

Categories of Gonad Condition

The following descriptions of the male and female developmental stages represent an attempt to divide the reproductive process (either spermatogenesis or oogenesis) into distinct phases. The criteria used are based solely on morphological observations. Categories comparable to those already in use for other species (ROPES & STICKNEY, 1965; BROUSSEAU, 1978, for *Mya arenaria*; PORTER, 1964; KECK, MAURER & LIND, 1975 for *Mercenaria mercenaria*) have also been used in the study where appropriate.

Developmental Stages of the Male

Indifferent Stage

The follicle is composed mainly of vacuolated, nutritive follicle cells, with a few spermatogonia scattered along the periphery or near the central axis. There were no pycnotic cells or multinucleated non-pycnotic cysts apparent in the follicles (Figure 1a).

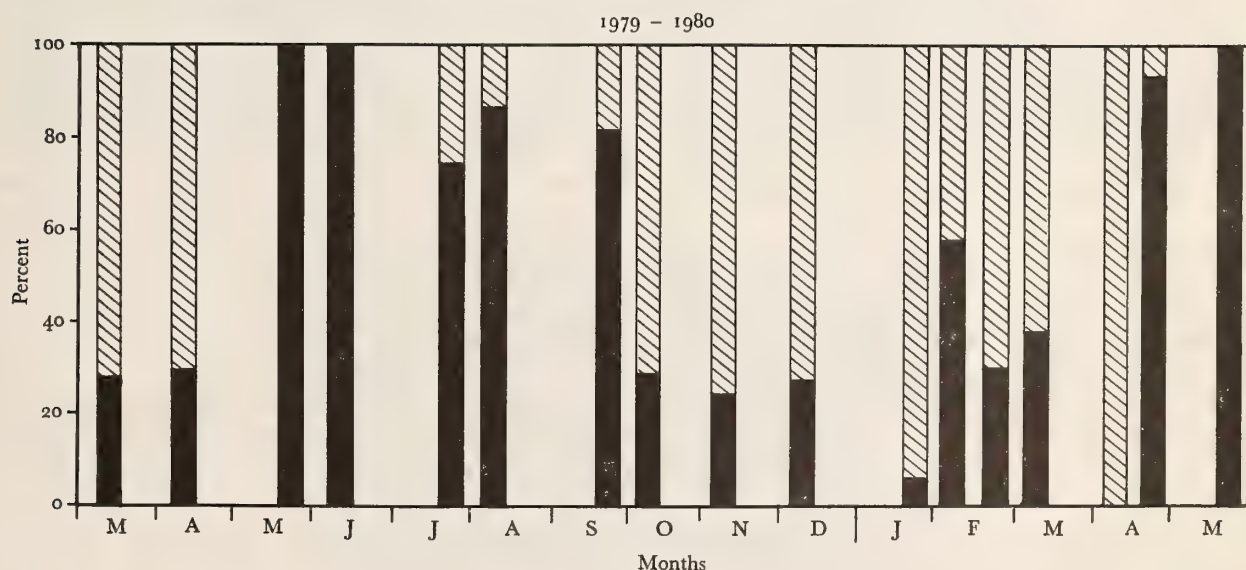


Figure 3

Proportions of *Petricola pholadiformis* population with active or inactive gonads during 1979-1980. Cross-hatched portions of each bar represent inactive gonads (indifferent, no gametogenesis, or spent); solid portions represent active gonads (developing, ripe gametes or partially spent). Observations on males and females are combined.

Developing Stage

As the spermatogenic cells proliferate, the follicle cells become less visible, declining in number and size as they supply nourishment for the increasing number of sex cells. The primary spermatocytes give rise to secondary spermatocytes which are rapidly transformed into spermatids. The spermatids then differentiate into spermatozoa which will appear as a dense mass in the lumen of the follicle of the ripe male (Figure 1b).

Ripe Stage

The mass of mature spermatozoa increases in volume and the individual cells arrange themselves in bands, with tails pointing toward the center of the lumen (Figure 1c).

Partially Spawned Stage

There is a marked decrease in the number of spermatozoa filling the lumen, accompanied by a reduction of the spermatogenic layer (spermatocytes and spermatids) (Figure 1d).

Spent Stage

In totally spawned males, a few residual sperm are visible in the lumen of the follicle. There is no evidence of active spermatogenesis taking place (Figure 1e).

Developmental Stages of the Female

Indifferent Stage

The follicles are intact and filled with follicle cells in the central area. Small oocytes with deeply staining, basophilic nucleoli are evident in the wall of the follicle. In some instances, inclusions are scattered throughout the follicle (Figure 2a).

Developing Stage

Oocytes become more noticeable along the follicle walls, increasing in size and number. The developmental phase is a continuous process, involving a proliferation and growth of the oocytes, with an accompanying decrease in the size of the follicle cells. The developing oocytes which begin as hemispherical or cylindrical-shaped cells attached to the wall of the follicle, become enlarged spherical cells 20 to 30 μm in diameter as full growth approaches (Figure 2b).

Ripe Stage

Ripe females are characterized by the presence of large, round oocytes, 40 to 50 μm in diameter, some of which are attached to the follicular wall by slender stalks. Others appear as free oocytes in the lumen of the follicle. The ripe oocytes contain large amphi-nucleoli within the lightly staining germinal vesicle (Figure 2c).

Partially Spawned Stage

There is a noticeable reduction in the number of ripe oocytes present in the lumen and some follicles are completely devoid of sex cells (Figure 2d).

Spent Stage

Clams which have recently undergone oogenesis can be recognized by the presence of a few unspawned oocytes in the lumen. These may be in varying degrees of cytolysis. Resumption of oogenic activity may be evident in some individuals (Figure 2e).

Reproductive Cycle

Reproductively active individuals (developing, ripe and spawning) were encountered throughout the 15-month

Explanation of Figure 1

Photomicrographs of gonadal stages of the male
Petricola pholadiformis

a) indifferent male, 14 March 1979; b) developing male, 11 April 1979; c) ripe male, 28 May 1979; d) partially spawned male, 14 June 1979; e) spent male, 15 October 1979 (all $\times 125$)

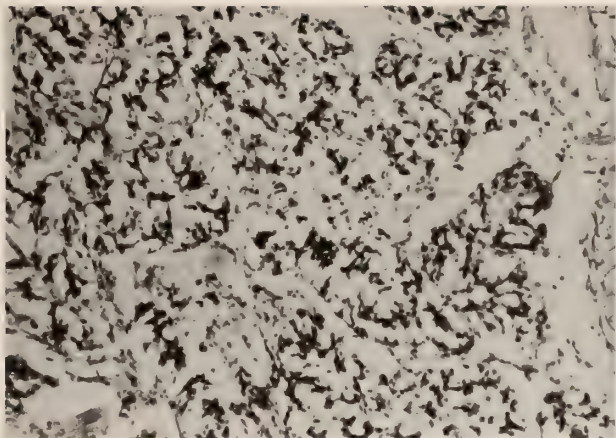


Figure 1a

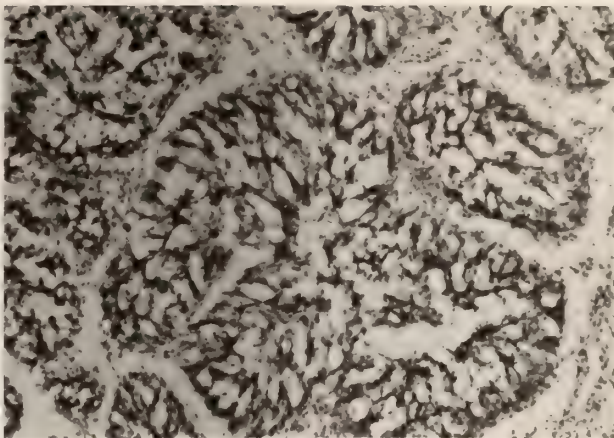


Figure 1b

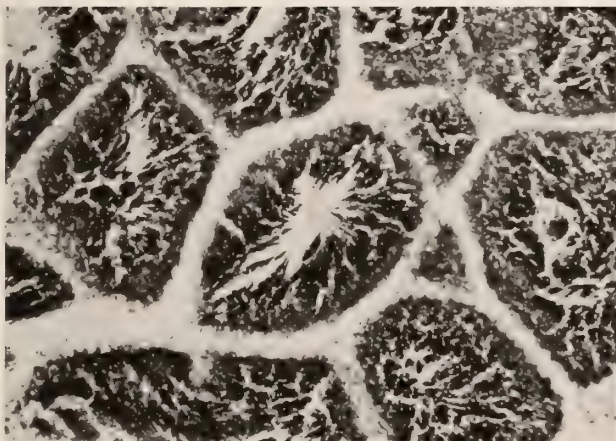


Figure 1c

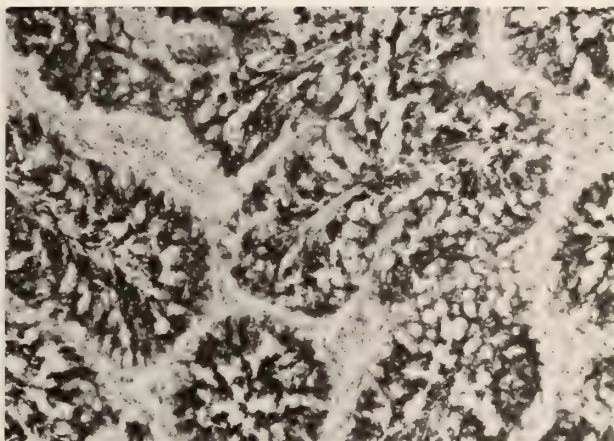


Figure 1d

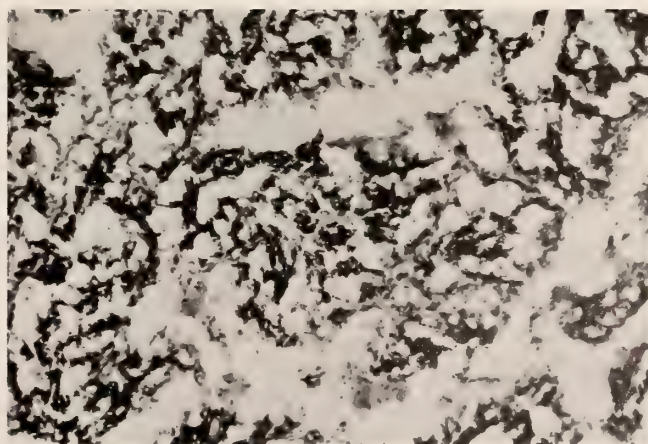


Figure 1e

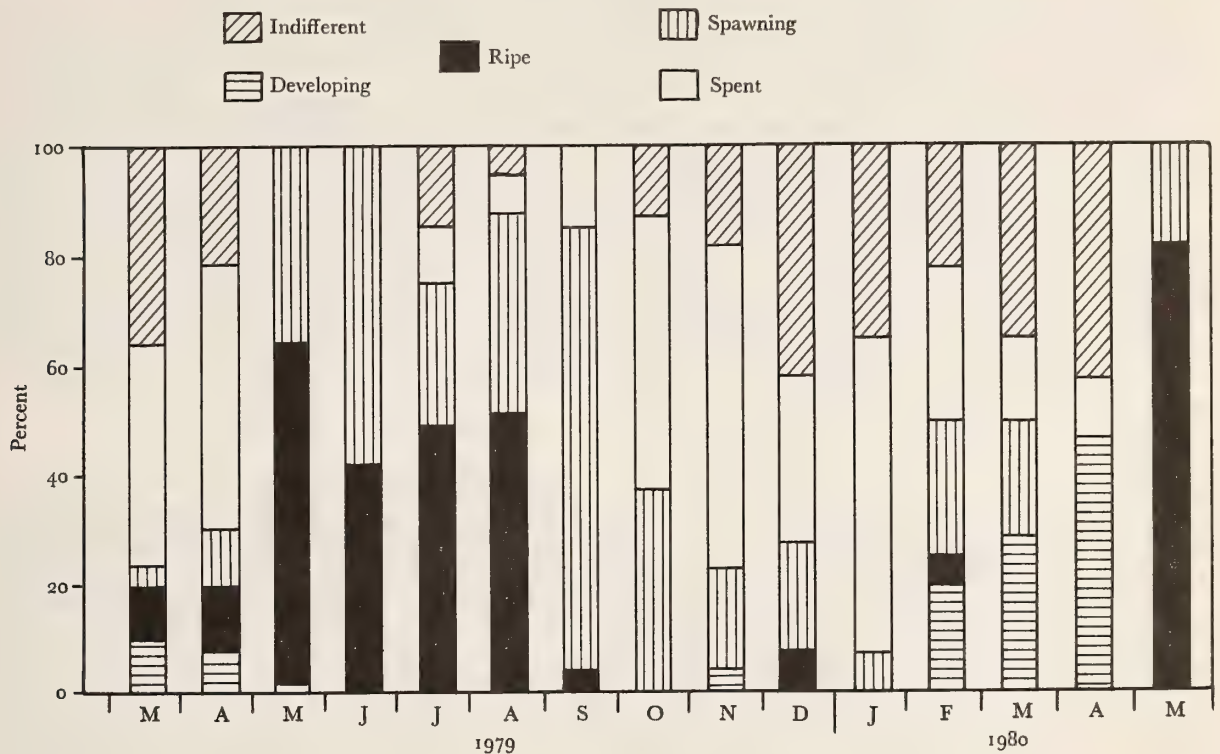


Figure 4

Proportions of *Petricola pholadiformis* population with gonads in each developmental phase during 1979-1980. Observations on males and females are combined.

study period, the largest numbers occurring in May and June of 1979 and April and May of 1980 (Figure 3). Gametogenesis began in February in both sexes (Figure 4). Although males containing scattered spermatozoa were present in all of the March and April samples in both years, no fully ripe males were encountered, while females possessing pockets of ripe oocytes were observed in some of the March and April samples in 1979. By May 1979, over 65% of the clams (both sexes) were found in a ripe condition. Discharge of eggs took place during the summer months. By mid-October approximately 50% of the clams had completely spawned and returned to the indifferent condition.

Sex Ratios and Fecundity

The reproductive potential of a population depends to a large extent on the number of fertile females and the number of young produced per female. In the population

studied, the proportion of females in all size-classes ($N = 489$) did not differ significantly from one-half. In size-classes < 15.0 mm, male and female gonads were indistinguishable. No evidence of hermaphroditism or protandry was observed. Trematode sporocysts (species undetermined) were found in the digestive gland and gonadal tissue of 11 individuals collected during the summer months, the highest incidence occurring in July, 1979. There was no morphological evidence to suggest sterilization of the host due to infection.

The number of oocytes produced was found to increase exponentially with increasing female body size. The regression equation for oocyte numbers (O) versus female shell length (S) is:

$$\log_{10} O = 2.651 \log_{10} S + 1.012$$

Females < 27.0 mm in length were never gravid. However, this may be due to limited sampling of size-classes < 25.0 mm.

DISCUSSION

The population of *Petricola pholadiformis* spawns once annually, during the summer months at Milford, Connecticut (Figure 3). Similarly, DUVAL (1963) reported that the main spawning period for these clams from southeastern England is during August. DUVAL (1963) also reported that the spawning period for the English population corresponded with the appearance of veligers there in the plankton. On the other hand, the presence of ripe and partially spawned clams earlier in the year (March-April) in the Milford population suggests that a more complex spawning pattern may be the case for some individuals within this latter population. However, without additional information on when the larvae of *P. pholadiformis* are present in the plankton in Long Island Sound or when the spat appear on the tidal flat, the existence of multiple spawnings cannot be substantiated.

Gonadal oocyte counts provide an accurate measure of fecundity in *Petricola pholadiformis* as in other species of bivalves where nearly total discharge of eggs occurs. Fecundity values for *P. pholadiformis* indicate that the largest females produce the largest number of oocytes. Average oocyte production by a 50.0 mm clam during a single breeding season is about 325 000. Although fecundity of *P. pholadiformis* is large, this estimate is considerably lower than the previous value of 3×10^6 eggs given by DUVAL (1963). Compared to other species of marine bivalves, *P. pholadiformis* occupies an intermediate position in the reported ranges: 120 000 for *Mya arenaria* (BROUSSEAU, 1978) to 10-20 million for *Crassostrea virginica* and *Mercenaria mercenaria* (GALTSOFF, 1930; DAVIS & CHANLEY, 1956). This high fecundity is probably an evolutionary safeguard against the unfavorable consequences produced by high mortality during pelagic life, metamorphosis and early settlement.

SUMMARY

A population of *Petricola pholadiformis* in Long Island Sound, Milford, Connecticut was studied for 15 months

to determine spawning frequency and fecundity under natural conditions. This population spawned during the spring and summer, mainly in June-August. Female body sizes (shell length) and oocyte production were positively correlated ($r = 0.62$). Sex ratios of *P. pholadiformis* 15-62 mm shell length, did not differ significantly from 1:1. In smaller individuals, male and female gonads were indistinguishable. No evidence of hermaphroditism or protandry were observed. A low frequency of trematode infestations of the visceral mass was reported during the summer months.

ACKNOWLEDGMENTS

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Explanation of Figure 2

Photomicrographs of gonadal stages of the female
Petricola pholadiformis

- a) indifferent female, 14 March 1979; b) developing female, 14 March 1979; c) ripe female, 28 May, 1979; d) partially spawned female, 18 July 1979; e) spent female, 11 April 1979 (all $\times 125$).

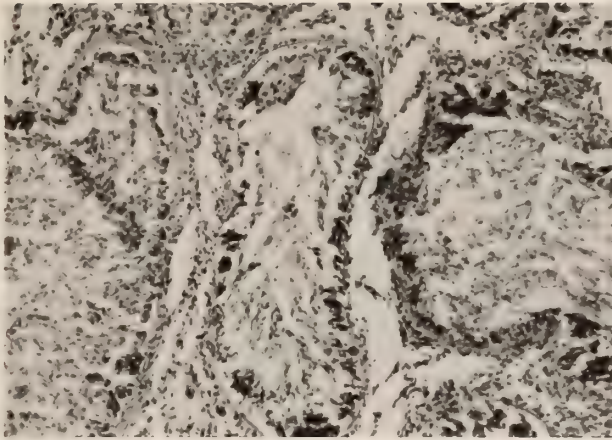


Figure 2 a

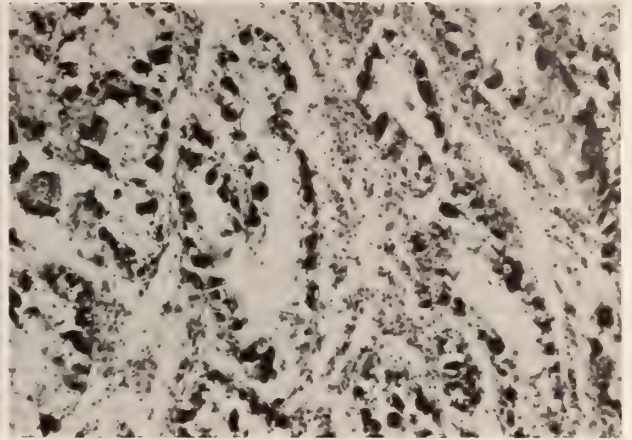


Figure 2 b

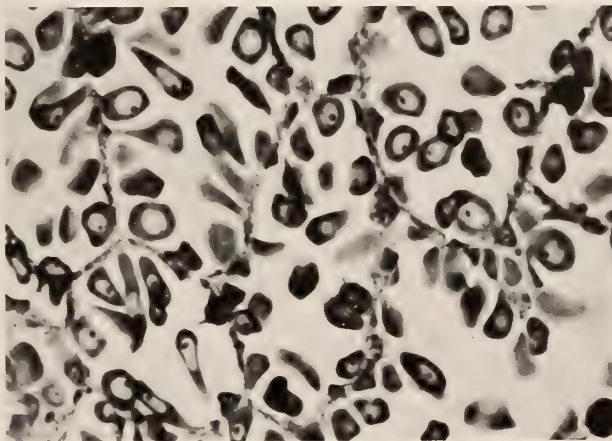


Figure 2 c

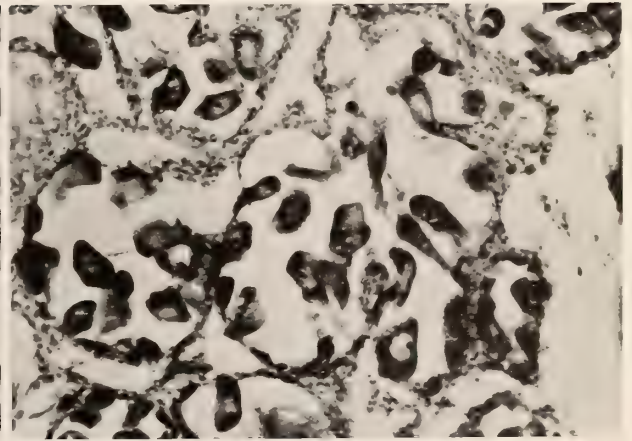


Figure 2 d

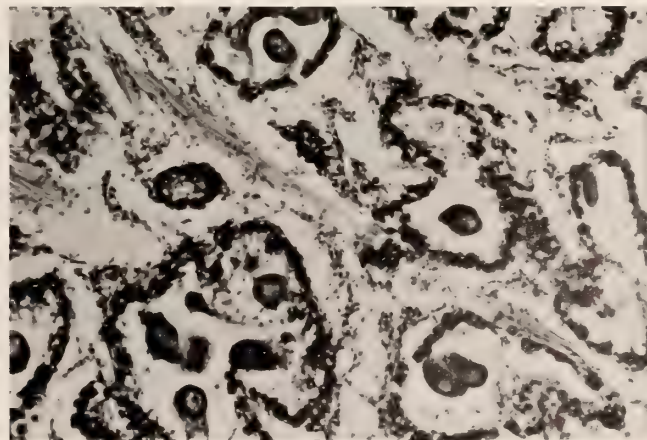
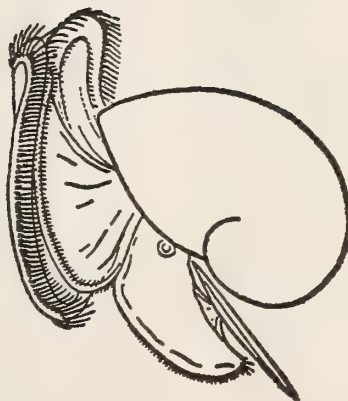


Figure 2 e

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Neptunea pribiloffensis (Dall, 1919)
and *Tealia crassicornis* (Müller, 1776):
On a Snail's Use of Babysitters

BY

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INTRODUCTION

BOREAL AND ARCTIC MARINE ANIMALS often have reduced planktonic larval stages compared with their temperate and tropical relatives (THORSON, 1935, 1950; FRETTER & GRAHAM, 1962; MILEIKOVSKY, 1971). This phenomenon is particularly well documented in prosobranch gastropods in northern seas, some of which have long encapsulated developmental periods: *Neptunea bulbacea* (BERNARDI, 1858), 3 to 4 months (GOLIKOV, 1961); *N. antiqua* (LINNAEUS, 1758), about 6 months (PEARCE & THORSON, 1967); and *Ceratostoma foliatum* (GMELIN, 1791), 120 days (SPIGHT, *et al.*, 1974). Prosobranchs may deposit their egg capsules in large masses, and while mesogastropods may protect their egg masses, neogastropods generally do not (ROBERTSON, 1974). The risks during long developmental times include mortality from predation and environmental variables (FRETTER & GRAHAM, 1962; FEARE, 1970; ROSENTHAL, 1970; EATON, 1971; MILEIKOVSKY, 1971; SPIGHT, *et al.*, 1974; SPIGHT, 1977). These mortality effects must certainly be proportional to the length of intra-capsular development. Certain populations of at least one species of northern whelk of the widespread neogastropod genus *Neptunea* appear to reduce these hazards by using a formidable babysitter. The females of an intertidal population of *Neptunea pribiloffensis* (DALL, 1919) near Homer, Alaska (59°38'N, 151°27'W) deposit their egg capsules in a large "corn-cob" shaped capsular mass near the relatively common large sea anemone, *Tealia crassicornis* (MÜLLER, 1776).

MATERIALS AND METHODS

For two years snails were counted in an area of the beach of about 2 ha, and the number of *Neptunea* females depositing egg capsular masses was noted. Band transects were surveyed in March, May, June, July, and September, 1979, with 100-500 m² surveyed per month, and two quantitative 0.25 m² infaunal samples were taken in both May and September, 1979, to determine population densities of *Neptunea pribiloffensis*, *N. lyrata* (GMELIN, 1791), *Tealia crassicornis*, and the green sea urchin, *Strongylocentrotus droebachiensis* (MÜLLER, 1776).

The diets of *Tealia* and *Strongylocentrotus droebachiensis* were surveyed by examination of the gastrovascular cavity of the sea anemone, and examination of the mouth and teeth of the sea urchins. Two *Neptunea pribiloffensis* capsular masses, several *Tealia* and several sea urchins were collected and returned to the laboratory where experiments were performed to see if the sea urchins would eat unprotected capsular masses, if *Tealia* could protect the capsular masses, and if *Tealia* could catch the sea urchin in the absence of the capsular mass. An aquarium was divided into two equal-area chambers and a capsular mass was placed in each chamber. A *Tealia* was placed in a randomly chosen chamber within 10 cm of the mass, and four starved sea urchins were placed in each chamber. The temperature was maintained at 4°-9°C, and the light-dark cycle was regulated to approximate natural conditions. Eleven experiments were run from February through May and during this period day length increases about 30 min/week at this latitude. The temperatures varied to approximate natural water temperatures. No

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correlations between the results of any of the laboratory experiments and the variations in the temperature and light regimes were noted. The experiments ran for one week or until the mass was attacked or an urchin was eaten. At the conclusion of the experiment, the *Tealia* and the sea urchins were removed and the experiment was repeated with fresh animals, whereas the capsular masses were reused. Additionally, 17 experiments were run with individual *Tealia* placed in empty chambers with four sea urchins. These experiments ran for one week or until a sea urchin was eaten.

To test the null hypothesis that proximity to *Tealia* had no effect on the survival of the capsular masses, I chose 16 intact *Neptunea pribiloffensis* capsular masses within 10 cm of *Tealia*; 12 *Tealia* with a single intact capsular mass and two *Tealia* with two capsular masses. Half of the *Tealia* were removed on 9 August, 1979, by randomly removing one of the *Tealia* with two capsular masses and six of the twelve with single masses. The sites were examined for survival of the masses on 6 September, 1979.

In the 1980 census, I collected and examined all 1979 capsular masses that I found, and 11 newly laid intact masses. The older capsular masses were easily distinguished by their heavy growth of diatoms and brown coloration, which contrasted with the brilliant yellow coloration of newly laid masses. The characteristic coloration of the older capsular mass takes about four to six months to acquire, consequently different year classes of capsular masses can be easily distinguished throughout the period when they co-occur. The number of intact egg capsules present, the length and width of the capsular mass, and the number of prehatching juveniles present (1979 capsular masses only) and any evidence of sea urchin predation were noted.

Differences between samples and experimental results were tested statistically with either the log likelihood ratio or a t-test, whichever was appropriate (SOKAL & ROHLF, 1969).

RESULTS

Not all *Neptunea pribiloffensis* females oviposit near *Tealia* and virtually no *N. lyrata* egg capsules were found near *Tealia*, even though several *N. lyrata* egg capsules were found in the censuses. These *N. pribiloffensis* masses not placed near *Tealia* were often deposited on the top of small (10-20 cm diameter) rocks in the area, though a few other masses occurred haphazardly in the region. The masses on the rocks sometimes passed the summer unscathed, but the advent of autumn and winter storms

causes large waves, some in excess of 4 m high, to strike the beach, rolling these small stones around. Few of the capsular masses on the stones survive the winter.

The morphology of the egg capsule group of *Neptunea lyrata* differs markedly from that of the capsular mass of *N. pribiloffensis*. *Neptunea lyrata* deposits capsules singly on a hard substrate close together and in a spiral pattern. *Neptunea pribiloffensis* cements its capsules together in a helically coiled tube to form a characteristic "corn-cob" shaped mass. *Neptunea lyrata* capsule groups are generally deposited on the undersides of rock ledges or in crevices. Both of these areas are refuges from sea urchins. *Neptunea pribiloffensis* can not deposit its large capsular masses in those areas.

Both species of *Neptunea* spawn in this area from late April through early June, and each female *N. pribiloffensis* takes about 2 or 3 days to deposit a complete capsular mass. In 1979, 27 of the 35, and in 1980, 32 of the 37 spawnings observed were laid within 10 cm of *Tealia*. *Tealia* density in the area is patchy, but seldom exceeds 2 m⁻², consequently the mean inter-*Tealia* distance is greater than 40 cm, and the above data represent a substantial deviation from a random distribution of capsular masses.

A single newly laid capsular mass was collected on 29 May, 1979, and maintained at 4°-10° C in the laboratory until March, 1980, when equipment failure terminated the experiment. At that time it contained prehatching, but somewhat immature juveniles. All of the 1979 capsular masses collected in 1980 contained prehatching juveniles, and as juveniles were observed hatching in June, 1979, from a mass laid the previous year, the developmental time for *N. pribiloffensis* appears to be about one year.

The mean length of the old capsular masses collected farther than 10 cm from *Tealia* was significantly shorter than the mean length of the new masses, and substantially shorter than the mean length of the old masses collected near a *Tealia*. Furthermore, the older masses collected away from a *Tealia* had torn and empty capsules on the upper edge, probably indicating that those capsules had been preyed upon. Although some of the masses collected near a *Tealia* showed some signs of predation, they were still larger than those collected far from a *Tealia*. More importantly, those masses near *Tealia* produced significantly more juveniles per egg capsular mass than did those found at a greater distance (Table 1).

Sea urchins, known predators on gastropod egg capsules (EATON, 1971; SPIGHT, *et al.*, 1974), are abundant, $11.24 \pm 11.06 \text{ m}^{-2}$, but were not often found feeding. Only 27 of 415 sea urchins examined were eating: 12 were eating polychaetes, 12 were eating algae, and 3 were eating

Table 1

Egg capsular mass survey results and probabilities.
Values are \pm one standard deviation. Dimensions in mm.

A. Survey results					
Capsular mass type	N	Egg capsular mass		Intact capsules	Juveniles
		Length	Width		
Newly laid (1980)	11	61.8 \pm 14.7	28.5 \pm 4.8	46 \pm 11	NA
Old (1979)					
Near <i>Tealia</i> (d \leq 10 cm)	5	45.1 \pm 6.2	33.5 \pm 5.6	18 \pm 10	46 \pm 24
Away from <i>Tealia</i> (d > 10 cm)	4	36.6 \pm 4.6	32.3 \pm 2.9	6 \pm 6	13 \pm 12
B. Probability of differences in means (t-test)					
Differences between:	df	Length	Intact capsules	Juveniles	
Newly laid					
Old—near <i>Tealia</i>	14	0.02 \leq P < 0.05	P < 0.001	NA	
Newly laid					
Old—away from <i>Tealia</i>	13	0.001 \leq P < 0.01	P < 0.001	NA	
Old—near <i>Tealia</i>					
Old—away from <i>Tealia</i>	7	0.05 \leq P \leq 0.10	0.05 \leq P \leq 0.10	0.02 \leq P \leq 0.05	

one *N. pribiloffensis* capsular mass at one of the *Tealia* removal sites. This survey was conducted at low water when the sea urchins were exposed, and these animals feed primarily when covered. Nonetheless, during the census period some sea urchins were seen eating *N. pribiloffensis* egg capsules. Of the 122 *Tealia* examined, 11 had eaten one *S. droebachiensis* each, and one each had eaten algal fragments, a bryozoan, a bivalve, and a compound ascidian; 107 had empty gastrovascular cavities.

In the laboratory experiments, *Tealia* can effectively prevent predation upon an egg capsular mass by a sea urchin. Of the 11 trials where a capsular mass was offered to sea urchins with no *Tealia* present, the mass was attacked 5 times; when *Tealia* was present, the mass was not attacked any of the eleven times. These differences are significant ($G = 4.630$; $0.025 \leq P \leq 0.05$). *Tealia* can eat the sea urchins whether or not the capsular masses are present. Eleven trials were run with a capsular mass present, and in one of these a single sea urchin was eaten. Seventeen trials were run without a capsular mass present, resulting in a single sea urchin being eaten in 5 of them. The remaining trials did not result in any sea urchins being eaten.

The field *Tealia* removal experiments also indicate the protective value of the sea anemone. Of the 8 masses

where the *Tealia* had been removed, 7 showed signs of predation within the month of the experiment. Four were completely eaten, leaving only the attached base of the capsular mass, and 3 were partially eaten. Of the 8 masses near a *Tealia*, only one was partially eaten. Comparing the two groups, with and without *Tealia*, for evidence of predation yields a highly significant difference ($G = 6.736$; $0.005 \leq P \leq 0.010$). In one case a green sea urchin was eating the capsular mass within a day of the sea anemone removal. In both the laboratory and the field, *Tealia* can protect the capsular masses from predation.

DISCUSSION

In spite of the fact that *Neptunea lyrata* hides its egg capsules from predators and *N. pribiloffensis* uses a formidable babysitter and can fledge relatively high numbers of juveniles per surviving capsular mass, recruitment into the area is poor. During the band transect and infaunal surveys, a total of 1125 *N. pribiloffensis* and 185 *N. lyrata* were seen and only one juvenile (shell length = 6.77 mm) *N. pribiloffensis* was seen. Thus, although spawning is frequent in the habitat, recruitment appears unlikely. Because of the long developmental time for these embryos,

selection for oviposition sites that ameliorate the predatory pressure must be very strong. *Neptunea lyrata*, by the virtue of the low capsular mass shape, can place its capsules in narrow spatial refuges that are unavailable to *N. pribiloffensis* because of its cylindrical capsular mass shape. A behavior resulting in selection of an oviposition site near a major sea urchin predator could certainly be advantageous for *N. pribiloffensis* if it resulted in significantly higher juvenile survival.

Those instances of partially eaten egg capsular masses near a *Tealia* indicate not only predation by sea urchins, but probably also indicate predation on sea urchins by the guardian sea anemones. Thus, the *Neptunea pribiloffensis*-*Tealia crassicornis* association may be mutualistic; the snail has a babysitter for its eggs, and the sea anemone has a bait to attract its major prey. Although laboratory experiments showed no significant baiting property of the capsular masses, this is probably an artifact of the relatively small confined space within the experimental aquaria. In nature, the sea urchins are seldom found concentrated close to *Tealia*.

Many associations of gastropods and cnidarians are known, but these generally involve predator-prey interactions (ROBERTSON, 1965; PERRON, 1978). This use of a sea anemone as a protector for gastropod embryos appears to be unique. The data presented here suggest *Neptunea pribiloffensis* developed this behavior in response to a long developmental time and predation on its eggs. Similar egg capsular masses are found in several species of *Neptunea* (*N. antiqua*, *N. beringiana* (Middendorff, 1848), *N. cumingii* (Crosse, 1862), *N. despecta* (Linnaeus, 1758)) (THORSON, 1935; GOLIKOV, 1961; AMIO, 1963; PEARCE & THORSON, 1967). Developmental times are unknown for most of them; however, the juveniles hatching from the capsules are generally large and probably require a developmental time on the order of several months. The developmental time shown here for *N. pribiloffensis* is the longest known for any boreal gastropod, although many of the above species may have developmental times of similar lengths. GOLIKOV (1961, 1963) is almost certainly in error in reporting developmental times of about a month for several of the species he examined, particularly *N. lyrata*. It appears he was working with both old and new capsular masses dredged at approximately the same time.

In light of the long developmental times expected, and capsular mass morphology of these species of *Neptunea*, behavioral patterns similar to those seen in *N. pribiloffensis* may occur in other species. As the egg capsular masses and developmental times are similar in many genera of

northern Buccinacea, the distributions of these snails may be correlated with the availability of appropriate "babysitter" and/or spatial refuges for egg capsule deposition.

SUMMARY

1. *Neptunea pribiloffensis* deposits its spawn near the relatively large anthozoan, *Tealia crassicornis*.
2. More egg capsules and significantly more juveniles survive the year-long developmental period from those capsular masses deposited near the sea anemone than from those deposited more than 10 cm away.
3. Laboratory experiments and field observations indicate the major cause of capsular mortality is predation by the sea urchin, *Strongylocentrotus droebachiensis*.
4. Observations and experiments support the hypothesis that *Tealia crassicornis* protects the capsular masses from predation by the sea urchins, by eating approaching sea urchins.
5. The importance of this or similar behavior patterns as related to egg capsular mass morphologies is discussed.

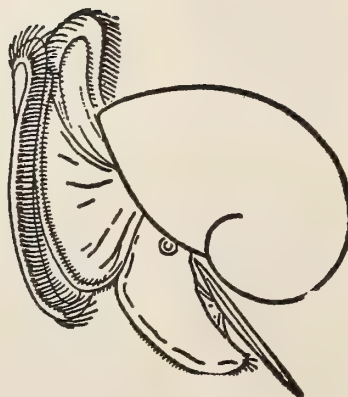
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On the Reproduction of *Epitonium rupicola* Kurtz

(Gastropoda : Epitoniidae)

BY

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(1 Plate; 1 Text figure)

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INTRODUCTION

THE BROWN-BANDED WENTLETRAP *Epitonium rupicola* (KURTZ, 1860) is a carnivorous marine gastropod that occurs in the western Atlantic from Cape Cod, Massachusetts, to upper Florida, and west to Texas (CLENCH and TURNER, 1951). It is rarely found intertidally but appears to be more common offshore down to a depth of about 50 meters. Although some aspects of its natural history may be inferred from the meager studies on related species, the biology and ecology of *E. rupicola* remain essentially unknown. ROBERTSON (1963) described the feeding habits of specimens collected in Delaware Bay, New Jersey, and he also reviewed the literature on feeding in other wentletraps. It is the purpose of this paper to describe the egg capsules of *E. rupicola* and to present some observations on its early development.

OBSERVATIONS

Three snails, each in the process of producing strings of egg capsules, were collected on three separate occasions (1960, 1962, 1963) from the muddy-sand flats of Delaware Bay, New Jersey (Table 1; Figure 1). The location was the same in each case, namely, in the extensive intertidal area south of Pierces Point and approximately 16 km north of Cape May Point (39°04.5' N; 74°54.9' W). They were collected by hand during low tide in shallow sloughs that run parallel to the shore about 75-100 m below the mean high tide mark. Water temperatures at high tide on each date were 25.5, 23.2 and 24.6° C, respectively; corresponding salinities were 20.2, 17.8 and 21.4 ‰. The flats were searched periodically throughout the spring, summer and fall of these and other years, but additional snails or egg capsules were not recovered. In 1968, another

Table 1

The number of egg capsules produced by *Epitonium rupicola* in the field and in the laboratory

Snail number	Date of collection	Location	Shell length (mm)	Number of egg capsules	
				Field	Laboratory
1	22-7-60	Delaware Bay, New Jersey	13.7	133	¹
2	21-6-62	Delaware Bay, New Jersey	17.2	76	20
3	19-6-63	Delaware Bay, New Jersey	16.0	123	66
4	3-7-68	Mouth of York River, Virginia	19.3	²	54
5	17-6-70	Gloucester Point, Virginia	³	126	—

¹Snail and capsules preserved on day of collection.

²Snail collected in a dredge; no capsules.

³Snail not collected.

Epitonium was dredged from several meters of water near the mouth of the York River, Virginia ($37^{\circ}14.7'N$; $76^{\circ}25.0'W$). A complete string of egg capsules, without the snail, was obtained several meters offshore in a bed of eelgrass (*Zostera*) at Gloucester Point, Virginia (York River) ($37^{\circ}14.7'N$; $76^{\circ}30.1'W$), in 1970. High water temperature on that date was $23.1^{\circ}C$ and the salinity was approximately 19 ‰. All snails and their capsules were brought to the laboratory, where they were placed in fingerbowls and observed. The snails will be referred to in the following text as numbers 1-5 (Table 1).

Snails in the process of forming egg capsules remain buried in the bottom so that the only evidence of their presence is the string of capsules on the surface. The string is extremely difficult to detect because each capsule is covered with silt and sand grains and closely resembles the substratum (Fig. 2). Upon casual observation, the string of capsules resembles a piece of debris or a branching bryozoan colony. Each string of capsules from the Delaware Bay snails was still attached to the snail, which indicates that the snails were still in the process of producing capsules, or if they had completed the process (possibly nos. 1 and 3, Table 1), the string is not released until some later time.

The numbers of egg capsules in strings produced by snails 1, 3 and 5 in the field may represent the normal range for completed strings. The string collected in 1970 must have been complete because larvae were emerging from all but two of the 126 capsules at the time of the collection.

After producing 123 capsules in the field, snail 3 deposited an additional string of 66 capsules in the laboratory approximately one month after it was collected. During this interval it was maintained under poor conditions (standing seawater, infrequent water change and no food). Hence, its 189 capsules may be only a minimum estimate of the reproductive potential of *Epitonium rupicola*. That this snail produced egg capsules in the laboratory suggests that under natural conditions more than one string of capsules may be produced during the reproductive season. Although the minimum length of time neces-

sary for a snail to produce a complete string of capsules is not known with any certainty, I did observe that the 54 capsules produced in the laboratory by snail 4 were laid within a 24-hour period.

The snail secretes a tough elastic string to which the capsules are attached. It is 0.06 to 0.20 mm in diameter, being thicker in the region of the capsules and tapering at the free ends. Neither sand grains nor silt are attached to the translucent string as it evidently lacks the sticky outer coating found on the capsules themselves. Apparently a short length of the string is secreted, and then the snail cements each capsule around the string as it continues to be secreted. The proximal end of the completed string is also devoid of capsules; apparently the string continues to be secreted after the formation of capsules is discontinued. Capsules are linearly arranged on the string in an alternate fashion so that they project from the string at angles of 90° - 130° or more from the next one on the opposite side. In some cases, there are series of three capsules, two of which project in the previous manner with another in between which may be 45° - 70° from the other two. This pattern is repeated along the string. It appears, therefore, that the capsules alternate in an arc of usually less than 180° , but the string becomes twisted to give an overall spiraled effect. The proximal end of each capsule touches the next. Snails, 1, 2, 3, and 5 produced strings of capsules that were approximately 50, 25, 50 and 56 mm in length, respectively (excluding the free ends of the strings). The length of the free ends of a string may total another 50 mm.

The capsules are cylindrical in shape, and round to oval in cross section (Figure 2). Their distal ends are rounded or somewhat flattened. The latter is an effect produced in some capsules by the coating of sand because capsules produced in clean dishes are all rounded distally. The proximal end of each capsule is drawn out into a nipple which completely surrounds the string (Figure 3). Each capsule does not fuse completely with the string because the latter can be pulled through the eye of the nipple. A few capsules on each end of the string are often somewhat stunted or misshapen. This phenomenon is usually seen in

Explanation of Figures 1, 2, 4, and 5

Figure 1: *Epitonium rupicola* no. 2 collected 21 June, 1962, in Delaware Bay, New Jersey. Scale = 5.0 mm

Figure 2: String of 76 egg capsules produced in the field by *Epitonium rupicola* no. 2; note the general arrangement of the capsules on one of the free ends of the string. Scale = 5.0 mm

Figure 4: Veligers of *Epitonium rupicola* within a flattened

capsule (produced in the laboratory) that are about ready to hatch. Scale = 0.2 mm

Figure 5: Veliger of *Epitonium rupicola* within an egg capsule (same as Figure 4) at high power magnification to show the conspicuous dark purple gland on the right side; one of the statocysts may also be seen. Scale = 0.05 mm



Figure 1



Figure 2

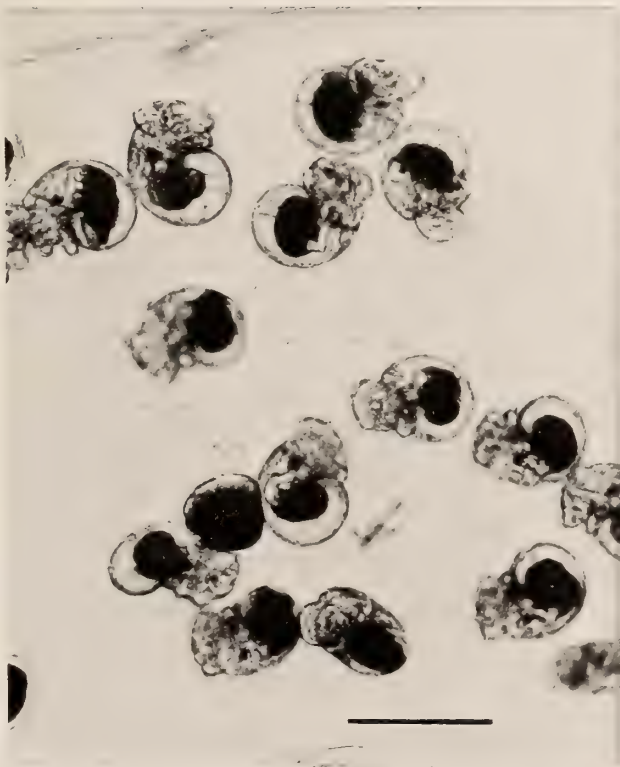


Figure 4

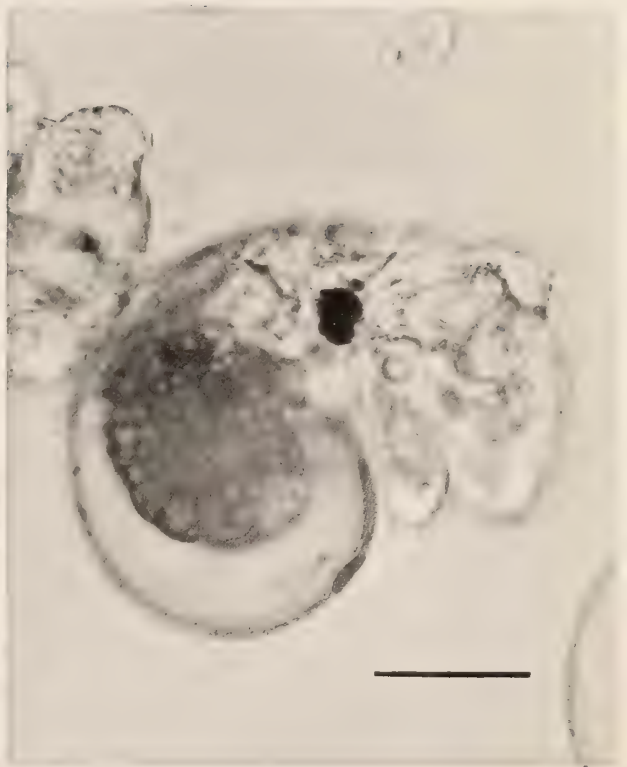


Figure 5

the strings of capsules produced by other gastropods (e.g., *Busycon*).

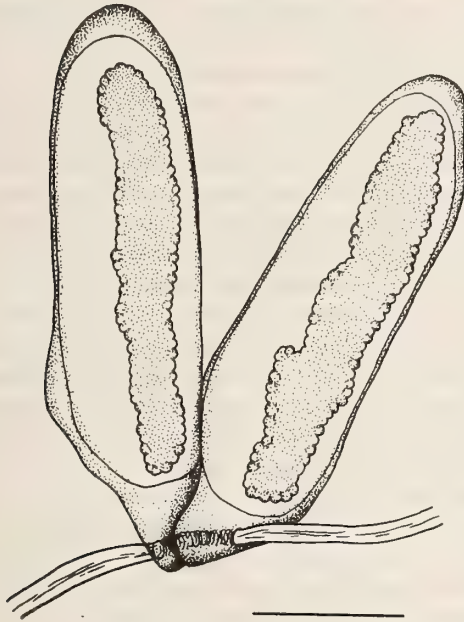


Figure 3

Two egg capsules from a string of 54 capsules produced in the laboratory by *Epitonium rupicola* no. 4; the capsules are less than 24 hours old and the embryos at this stage tend to adhere to one another. Scale = 1.0 mm

The mean length of the capsules produced by individual snails appears to vary directly with the size of the snail, but the shape of the capsules is consistent. I measured ten capsules from each of three preserved strings produced in the field. Capsules from the smallest snail (no. 1) had a mean total length of 2.72 mm (range 2.22 - 2.88 mm). Capsules of snail 2 were 3.28 mm (3.19 - 3.45 mm) in length, and those from no. 3 were 3.48 mm (range 3.11 - 3.70 mm). Two capsules from no. 5, with unhatched veligers, were both 3.21 mm long. The mean diameter (width) of ten capsules from no. 2 was 1.09 mm (range 0.97 - 1.14 mm); the maximum diameters of the two capsules from no. 5 were 1.03 and 1.08 mm. In summary, the capsules are approximately 2.5 - 3.5 mm in total length and about one-third as wide. Capsules produced by snails in clean dishes of seawater are understandably shorter and narrower be-

cause they lack sand grains. One such capsule produced by snail 2 was 2.75 by 0.95 mm. Capsules deposited under the same conditions by the largest snail (no. 4) were all approximately 3.7 mm in total length. If sand grains were attached, these would have exceeded the length of all others.

The basic construction of the capsules can be perceived only in those produced by snails in clean dishes devoid of particulate matter. The capsules are cylindrical with rounded ends, and completely transparent. The outer layer is especially thickened distally and near the base (Figure 3). It is initially very adhesive but becomes less so as it hardens. A thin membrane encloses the inner egg-bearing part of the capsule. It appears unlikely that snails, under natural conditions, mechanically manipulate sand grains and cement them to the capsules. Furthermore, it is doubtful that sand grains of uniform sizes are in any way selected by the snails as has been suggested for other species of Epitoniidae (FRETTER & GRAHAM, 1962: 402). It is most likely that the capsules are fortuitously covered with whatever particulate material occurs in the substratum housing the snail. Capsules of *Epitonium rupicola* were covered with sand grains of various sizes, texture and mineralogy. Where there are only a comparatively few sand grains on an individual capsule, the rest of the capsule is covered with silt.

The fertilized eggs are in a viscous, albuminous fluid, usually clumped in the recently formed capsule, and become separated as development proceeds. The numbers of eggs in three randomly selected capsules from snail 4, were 339, 400 and 554 (mean 431). A snail producing 125 capsules in one egg-string with an average of 400 eggs per capsule, has the potential of producing 50 000 veligers.

Periodic observations were made on the development and hatching of the veliger larvae, but no attempt was made to bring the larvae to metamorphosis. Capsules from snail 2, collected on 21 June 1962, were kept in a 11.5 cm diameter fingerbowl, and the water was changed daily (salinity approximately 25‰; water temperature 20 - 22°C). Four days later there were motile shelled veligers in the capsules, and large numbers emerged on 29 June (Figure 4). Each capsule had an opening at the distal end, and on some an irregular flap of the capsular wall was attached near the opening. The remainder of the veligers hatched on the following day. Three randomly selected capsules preserved before hatching contained 247, 376 and 549 veligers (mean 391). Two capsules from snail 5 contained 335 and 358 veligers. Twenty recently hatched, preserved veligers (from snail 2), measured with a calibrated ocular micrometer, had a mean shell length of 0.160 mm (range 0.152 - 0.163 mm).

Snail 4 produced an egg-string on 31 July 1968 after nearly a month in the laboratory (Table 1). The capsules were removed immediately to a clean fingerbowl with water maintained at approximately 24°C and 20‰ salinity. On 3 August ciliated larvae were rotating slowly within the capsules, and two days later veligers were beginning to hatch. Large numbers were in the dish on the following day. Thus, the developmental period under these laboratory conditions was five days. Again the veligers emerged from irregular openings at the distal ends of the capsules. The mean shell length of 20 veligers was 0.153 mm (range 0.139–0.166 mm).

Shells are smooth and transparent but the umbilical region is darkened. Veligers possess a slightly bilobed velum, two eyes, two statocysts, an operculated foot, and a distinct irregular dark purple mass (roughly 10–15 μ m in dia.) on the right side (Figure 5). This is probably the rudiment of the pigmented hypobranchial gland of the adult. THORSON (1964) described a similar structure in the same location in recently hatched larvae of *Epitonium* (*Clathrus*) *turtonis*, which he called an excretory organ. He also pointed out its resemblance to a similar structure in the cephalaspid, *Philine*.

DISCUSSION

The egg capsules of very few species of wentletraps have been described. CLENCH & TURNER (1951) said, in reference to the capsules of the genus *Epitonium* that, "So far as known the eggs are laid on a string of chitinized material and covered by agglutinated sand grains. The egg mass appears as a minute string of beads." They illustrated these statements by reference to a photograph of capsules produced in the laboratory by *Epitonium humphreysii* Kiener, collected from Pine Island Sound, Captiva Island, Florida. The bead-like shape of these capsules, however, is not characteristic for all members of this family.

VESTERGAARD (1935) described and illustrated the string of triangular egg capsules of *Scalaria communis* (Lamarck) [= *Epitonium* (*Clathrus*) *clathrus* (L.)] from Frederikshavn, Denmark. THORSON (1946) suggested that her snails were not *S. communis*, but were *Scala* (*Scalaria*) *turtonis* (Turton) [= *E. (Clathrus) turtonis* (Turton)]. He did not see Vestergaard's specimens, but based his conclusion on the fact that *E. turtonis* was more common in the sandy areas of Frederikshavn, and that the egg capsules of this species, which he collected in the same area, were similar to those described by her. LEBOUR (1937) described the egg capsules of *Clathrus clathrus* [= *Epitonium* (*Clathrus*) *clathrus*] from Plymouth, England as irregularly polygonal

and therefore different from those described by Vestergaard. However, although Vestergaard illustrated capsules that were very triangular, she also mentions that other strings may have more obtuse capsules. Furthermore, many of the capsules illustrated by Lebour were triangular or pyramidal in shape and looked very similar to some of those illustrated by Vestergaard and Thorson. This question is still unsettled, however, because FRETTER & GRAHAM (1962: Figure 211; p. 402) illustrated a portion of a string of capsules, collected in the Scilly Isles and identified as "*Clathrus clathrus*" [= *Epitonium clathrus*], which had pyramidal capsules very similar to those figured by Thorson for *E. turtonis*. Therefore, the real differences between the capsules of the two species is still not clear.

The capsules of *Epitonium humphreysii* Kiener (CLENCH & TURNER, *op. cit.*) are irregularly polygonal to rounded and certainly less angular than the European species mentioned above. Furthermore, their arrangement along the string is irregular compared to the more orderly arrangement of European forms.

HABE (1943) illustrated and described the egg capsules of *Habea inazawai* Kuroda. They are ellipsoidal, translucent, reticulately sculptured, and measure 1.8 by 1.2 mm. Apparently there are no sand grains attached to the capsular surface. He stated that there are more than 10 capsules in a mass, and these are held together by an elastic thread. They do not appear to be linearly arranged on the thread as is the case in the species mentioned above.

BOSCH (1965), in his description of the parasitic relationship between *Epitonium ulu* Pilsbry and the solitary coral *Fungia*, referred to the "small white eggs" of the snail which were attached to the coral. It appears evident from his photograph that he was probably referring to egg capsules rather than eggs. Unfortunately, he gave no further information on the nature of these capsules. THORSON (1958) mentioned that he found egg-strings attached to *Epitonium tinctum* (Carpenter) in southern California, but he did not provide any further information. The cylindrical capsules of *E. rupicola* are distinct, therefore, from all of the other species.

LEBOUR (1937) noted that *Epitonium clathrus* produced its string of capsules while completely buried in the substratum; the mass of capsules were on the surface and one end of the string was attached to the snail. VESTERGAARD (1935) observed the same phenomenon in the laboratory with what was apparently the same species. *Epitonium rupicola* behaves in a similar manner.

The reproductive potential of wentletraps can be determined only by careful field and laboratory study. The number of egg capsules attached to an individual snail collected in the field may or may not represent the ultimate

number which would have been produced had the snail not been disturbed. Whether or not a snail produces more than one egg-string during a season is likewise uncertain. Three specimens of *Epitonium rupicola* produced strings of egg capsules in the field that had 123, 126 and 133 capsules (Table 1). These totals may be compared with the 160 for *E. turtonis* (THORSON, 1946), and the 170 for *E. clathrus* (FRETTER & GRAHAM, 1962), both of which were field determinations. LEBOUR's (1937) string of capsules, which was illustrated only, contained approximately 160 capsules of *E. clathrus* (my count). Just as the shape of the egg capsules is related to the species, it is probable that the number of capsules and the length of the whole mass may also vary with the species. Variation within the species may be related to the size of the snails and the time during the spawning season (if more than one string is produced in a season). Limited data for *E. rupicola* indicate that the mean size of the capsules may be positively correlated with the size of the snail. The time for development to hatching in *E. clathrus* and *E. rupicola* also differs. In the former it is 9-14 days based on the combined observations of VESTERGAARD (1935) and LEBOUR (1937), while it is 5-8 days in *E. rupicola*.

The hatched veligers of *Epitonium rupicola* are similar to those of *E. clathrus* (VESTERGAARD, 1935) and *E. turtonis* (THORSON, 1946). Vestergaard's veligers were 0.15 mm long and Thorson's were 0.18 mm. Both investigators measured larvae hatched in the laboratory, but neither indicated how many were measured. The mean length of 40 veligers of *E. rupicola* measured on the day of hatching (20 from each of two snails) was 0.156 mm (range 0.139-0.166 mm). The reddish-brown umbilicus, the velum and the purple gland on the right side of the veliger characterize *E. turtonis* and *E. rupicola*. Neither Vestergaard nor Lebour, however, mentioned this purple structure in the veligers of *E. clathrus*. Thorson called this structure an excretory organ. The substance in this organ of the veliger has the same color as the material exuded from the hypobranchial gland of the adult *E. rupicola*. HABE (1943) briefly mentioned the purplish color of the fully developed veliger within the capsule of *Habea inazawai*.

ACKNOWLEDGMENTS

I am indebted to the late L. A. Stauber (Rutgers—the State University of New Jersey) for bringing to my attention the first specimen of *Epitonium rupicola* and its egg capsules. My appreciation is also extended to H. H. Haskin

for providing me with research facilities at the New Jersey Oyster Research Laboratory of Rutgers University. I also thank W. J. Hargis, Jr. for the use of the facilities at the Virginia Institute of Marine Science during the summer of 1968 and 1970. I am grateful to L. L. Sweat, of the same institution, for reproducing the prints from my original color slides.

SUMMARY

Egg capsules of *Epitonium rupicola*, found for the first time in an intertidal area of Delaware Bay, New Jersey, and the York River, Virginia, U.S.A., are described. While buried in the substratum, this snail produces strings of sand-covered, cylindrical capsules during June and July. Transparent egg capsules are produced by these snails in clean dishes in the laboratory, and development of the eggs to the veliger stage may be observed through the capsular wall. Veligers hatch in from 5 to 8 days through openings produced in the distal ends of the capsules. The veliger stage is described briefly and shown to be similar to that of some other species within the family. Capsules and veligers are compared with the descriptions of other members of the Epitoniidae.

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Investigation into Interspecific Encounters of the Sea Hare

Aplysia dactylomela Rang, 1828

(Gastropoda : Opisthobranchia)

BY

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(1 Text figure)

INTRODUCTION

SEA HARES of the genus *Aplysia* (Gastropoda: Opisthobranchia) have become the targets of intense investigations by neurophysiologists (see KANDEL, 1979 for review), yet, until recently, little has been known concerning the behavioral ecology of these molluscs. Field studies that have been done in the United States have been performed predominantly on *Aplysia californica* Cooper, 1863 (WINKLER, 1959; WINKLER & TILTON, 1962; KUPFERMAN & CAREW, 1974; AUDESKIRK, 1979).

Studies on *Aplysia dactylomela* Rang, 1828 have been much more limited. TOBACH *et al.* (1965) examined inking in *A. dactylomela*; and LEDERHENDLER *et al.* (1975) and TOBACH (1978) looked at aggregation and ecological adaptations of *A. dactylomela* in the Bahamas. More recently, DiMATTEO (1980a, b) has looked into inking, and its role as a defensive mechanism in *A. dactylomela* from Florida waters.

Information is at a minimum concerning the life history of this animal, especially where interspecific encounters are concerned. While *Aplysia dactylomela* appears to lead an adult life free of most predation, there are reports of predators feeding on *A. dactylomela* (see DiMATTEO, 1980a for review). Any type of quantitative examination in this area is however, woefully lacking. The data presented here are the results of a study designed to investigate more accurately the behavioral ecology, and the strategies employed by these soft-bodied molluscs in avoiding predation.

The experiments were set up to determine if *Aplysia dactylomela* would respond in a defensive way to the presence of carnivorous prosobranch gastropods, and echinoderms known to cause withdrawal responses in other gastropods. Since LEDERHENDLER *et al.* (1975) found an

avoidance to the cnidarian *Cassiopea xamachana* Bigelow, from sea hares in the Bahamas, this was also checked to see if this population of sea hares reacted in a similar manner.

METHODS AND MATERIALS

The study was performed at Pigeon Key, and Bahia Honda State Park, of the lower Florida Keys, U.S.A. Sea hares were collected from shallow water grass flats which border most of this area. Sea hares were maintained in recirculating salt water tanks. All sea hares were tested within one day of collection.

In the first experiment, sea hares were exposed to one of 5 different test animals. These test animals were (1) the predatory gastropod *Fasciolaria tulipa* (Linnaeus, 1758) (sizes ranged from 5.1 - 10.5 cm); (2) the asteroid *Echinaster sentus* (Say); (3) the holothuroidean *Astichopus multifidus* (Sluiter); (4) the herbivorous gastropod *Strombus gigas* (Linnaeus, 1758); and (5) empty *Fasciolaria* shells. Groups 4 and 5 were used as controls. The empty *Fasciolaria* shells were prepared by removing the animal or obtaining already empty shells. Shells were then boiled, soaked and rinsed in alcohol, and dried. The sizes of the shells were similar to the living *Fasciolaria* used.

Each sea hare was placed in an aquarium, and one of the five test animals was introduced. More than one test animal would be introduced to ensure that the sea hare would make contact. The order of presentation of the test animals was randomized throughout the experiments.

Results from the above trials were analyzed using the χ^2 test with $p < 0.05$. Each category was arranged in the order of the number of withdrawals shown by the sea

hares, and compared to the next. The categories were also lumped within each group and tested as well.

Trials with *Cassiopea* were performed in the same manner as discussed above, and four treatments were tested: (1) live *Cassiopea*; (2) *Cassiopea*, previously ground and placed on a glass rod; (3) *Cassiopea*, previously ground, to which 10% acetic acid was added to act as a stimulus for discharge of nematocysts, placed on glass rod; and (4) glass rod, no *Cassiopea* (control). In 2 and 3 above, *Cassiopea* were ground in a bowl with a pestle. The consistency of the mixture was such that it would cling to the glass rod. This would then be placed in front of a moving sea hare, or gently touched to the anterior of the sea hare. Data from this set of trials were also examined by χ^2 , with $p < 0.05$.

RESULTS

Results from the first set of trials are shown in Table 1. Figure 1 shows the categories set up as 3 groups, each group being significantly different from the other two in the number of withdrawals. Categories within each group are not significantly different from each other.

The control group consisted of the empty *Fasciolaria* shells, and the living *Strombus*. The number of withdrawals by the sea hares for this group was significantly lower than those of the other two groups, when tested separately, and when lumped together and tested.

The *Fasciolaria* categories are designated as group I. This group differed significantly from the control group ($\chi^2 = 6.66$), and from group II ($\chi^2 = 13.75$). While the two *Fasciolaria* categories were run at different times with

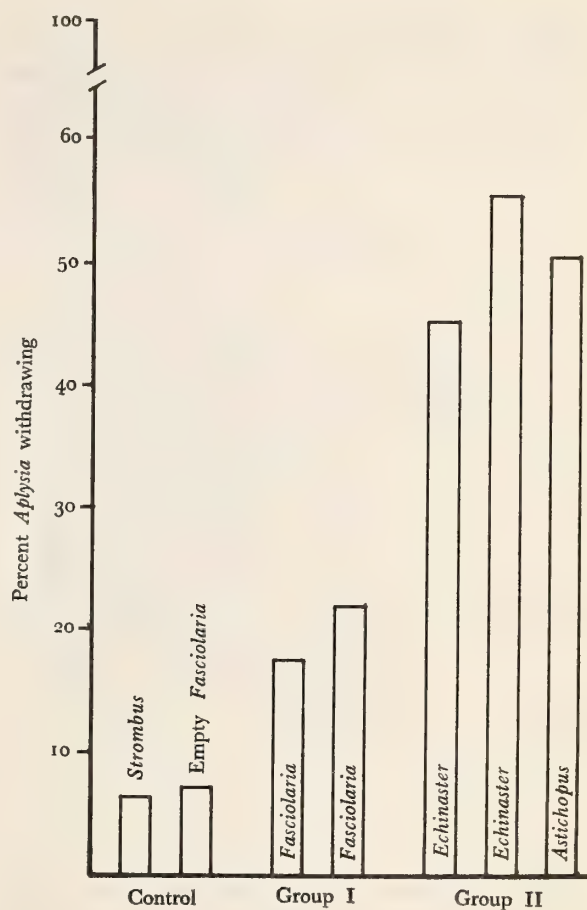


Figure 1

Withdrawal rates by *Aplysia* to the various test animals, arranged into three significantly different groups

Table 1

Results showing the number of withdrawals by *Aplysia dactylomela* when encountering the various test animals used in the trials

Response of <i>Aplysia</i>	Source of stimulus						
	<i>Strombus</i>	Empty <i>Fasciolaria</i> ¹	<i>Fasciolaria</i>		<i>Echinaster</i>		<i>Astichopus</i>
	Date:	4/79	7/80	4/79	7/80	4/79	7/80
Number of trials	50	85	50	85	50	55	70
Number of <i>Aplysia</i> withdrawing	3	6	11	15	28	25	36
Percent of <i>Aplysia</i>	6.0	7.1	22.0	17.6	56.0	45.5	51.4

4/79—Number of sea hares tested = 10; 7/80—Number of sea hares tested = 16

¹refers to cleaned shell, no animal (see text for preparation)

different animals (see Table 1), no significant difference existed between them.

Group II consisted of the echinoderms *Echinaster* and *Astichopus*. These test items all received high numbers of withdrawals by the sea hares. The difference between the two *Echinaster* categories is not significant ($\chi^2 = 0.98$).

Table 2

Results showing the number of withdrawals by *Aplysia dactylomela* when encountering *Cassiopea*

Response of <i>Aplysia</i>	Source of stimulus ²			
	Control	A	B	C
Number of trials	92	81	76	75
Number of <i>Aplysia</i> withdrawing	11	62	66	24
Percent of <i>Aplysia</i>	11.9	76.5	86.8	32.0
$X^2 = 55.32$, $df = 3$, $p = 0.05$				

Number of sea hares tested = 15

²Control—glass rod; A—glass rod/*Cassiopea*; B—*Cassiopea*; C—glass rod/*Cassiopea*/acetic acid.

Table 2 shows the results from the *Cassiopea* trials. The sea hares did withdraw significantly higher with contact by *Cassiopea*. No difference was observed between the sea hares' response to the live *Cassiopea* and the glass rod/*Cassiopea* mixture ($\chi^2 = 0.12$). The number of withdrawals from the glass rod/*Cassiopea* mixture, and the glass rod/*Cassiopea* acetic acid mixture, were significantly different with $\chi^2 = 16.79$.

DISCUSSION

Results from the first set of trials (Figure 1) provide the first experimental evidence indicating an escape response by *Aplysia dactylomela* towards predatory gastropods. Previous work (KANDEL, 1979) has shown an escape response by *A. californica* upon contact with the asteroid *Astrometis sertulifera*, with the stimulus appearing to be mechanical rather than chemical. The response shown by *A. dactylomela* in this study was similar to that described for *A. californica*. The stimulus here was also mechanical, and

this author agrees with KANDEL (1979) that the withdrawal seems to be caused by the pinching action of the pedicellaria of the starfish. The response of the sea hare to the sea star was virtually identical to that described by HENING *et al.* (1976); *i.e.*, a quickened crawling, with rapid pedal waves, much quicker than for routine crawling. The case for this mechanical stimulus was strengthened by exposing the sea hares to the holothuroidean *Astichopus multifidus*. The sea hares' responses were similar to those described for their reaction toward the asteroid. While *Astichopus* does not possess pedicellaria it is extremely warty and covered with protuberances considered to be sensory. The sea hares appeared to be undaunted by the presence of *Astichopus* until contact was made, then withdrawal was observed. *Astichopus* is a strict deposit feeder, thus it would not be of any advantage of the sea hare to show an escape response due to chemical signals from this animal. While *Echinaster* is omnivorous, it probably does not pose much of a threat to adult *Aplysia*. Thus, this mechanical stimulus may be more than adequate to deter sea hares. It should be interesting to examine the responses of *A. dactylomela* to some of the more voracious predatory sea stars, and chemicals emitted by them.

Fasciolaria tulipa is molluscivorous, and a very voracious predator in the Florida Keys. While the sea hares would often make contact with *Fasciolaria*, the exact stimulus eliciting the escape response is unclear. Given the importance of chemicals as mediators of molluscan escape responses (see MACKIE & GRANT, 1974 for review), it would seem likely that chemicals play some role in this case as well.

The results from the *Cassiopea* trials concur with those of LEDERHENDLER *et al.* (1975) for *Aplysia* in the Bahamas. In this study, sea hares reacted to contact with *Cassiopea* by rapidly withdrawing and turning away. The stimulus appeared always to be tactile, and as the trials with the acetic acid indicates, was most likely caused by the nematocysts present on the *Cassiopea*. Similar withdrawal responses have also been observed in *A. dactylomela* to contact with the gastropod *Cymphoma gibbosum* (DiMatteo, unpublished data), a species feeding exclusively on gorgonians bearing nematocysts. The response of the sea hare was always the same rapid retraction of the anterior end, with the sea hare turning or moving in a wide arc around the *Cassiopea*. This response was highly stereotyped for all sea hares tested.

This study quantifies and substantiates impressions given from casual observations in past literature. It should come as no surprise that *Aplysia dactylomela* shows some

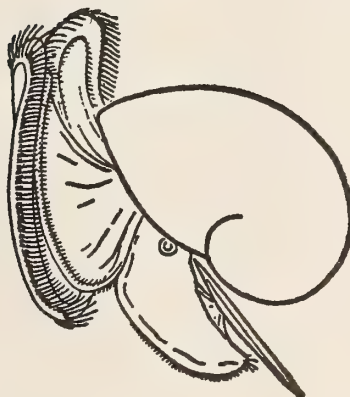
of the escape responses so common in opisthobranchs. *Aplysia dactylomela* is endowed with many mechanisms making it unpalatable to many predators, and together with the escape responses discussed in this paper, allow it to avoid much predation in the Florida Keys as adults.

ACKNOWLEDGMENTS

I wish to thank the staffs at both Pigeon Key, and Bahia Honda State Park for their cooperation during my stay there. I also wish to extend my thanks to P. Weldon for constructive comments on this manuscript.

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METHODS & TECHNIQUES

Nembutal for Narcotisation of Mollusks

BY

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THE TIME-HONORED METHOD of killing land mollusks for preservation is by drowning in water. Small animals can be drowned in a tightly capped container full of water at room temperature in about 12 hours. At least 24 hours are required to drown large specimens. A "half-drowned" snail or slug may appear dead, but will later contract into an undesirable position or slime excessively when placed in fixative or preservative. An "over-drowned" specimen decomposes rapidly. Obviously, narcotisation of freshwater mollusks will require additions of chemicals to the water.

The use of nembutal (sodium pentobarbitone) for the relaxation of mollusks was first suggested by VAN DER SCHALIE (1953). RUNHAM *et al.* (1965), in their review of narcotising methods, pointed out that nembutal as a 0.08% solution, was suitable for most mollusks with relaxation times of 12 to 55 hours. These authors found that nembutal was unsatisfactory for slugs (Limacidae, Milacidae, Arionidae) and suggested the addition of 1% propylene phenoxetol to the nembutal solution. MEIER-BROOK (1976) described an improved technique in the use of pentobarbital acid for relaxation of many freshwater snails and indicated its superiority over nembutal as a narcotising agent.

During the past few years I have found nembutal particularly useful in narcotisation of many freshwater and terrestrial mollusks prior to fixation and preservation. The technique used is essentially that of MEIER-BROOK (1976), but nembutal is employed instead of pentobarbital. The mollusks are placed in glass vials which are then filled completely with tap water. A small quantity of nembutal (crystalline) is transferred to the vial on a moistened spatula, the cap added and the whole briefly shaken to disperse the nembutal crystalline powder.

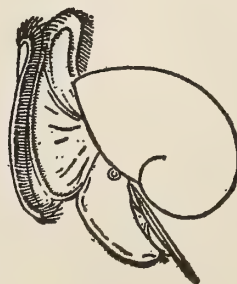
I have found with a large species range of freshwater and terrestrial mollusks that fixation and preservation can safely be carried out after 15 to 18 hours narcotisation, without contraction of the animal. Snails narcotised in nembutal and fixed in formalin (1 hour) can be extracted intact from the shell before preservation in alcohol.

Used in this way, nembutal is suitable for narcotisation of mollusks during field excursions. On return to the camp in the evening, the collected mollusks are transferred to vials and nembutal powder (crystalline) added. Before leaving camp in the morning, these mollusks are fixed and preserved.

My observations do not support previous contentions that nembutal must be maintained at a definite concentration, 0.05 to 0.1% (*e.g.*, RUNHAM *et al.*, 1965; MEIER-BROOK, 1976). The adequate amount of nembutal required for total relaxation is found after a short time of experience. Even a tiny amount is sufficient provided it is well dispersed. The use of nembutal is considered suitable for narcotisation of all pulmonate species (Basommatophora, Systellommatophora, Stylommatophora).

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NOTES & NEWS

A Note on the Occurrence of
Lithophaga (Leiosolenus) spatiosa
(Carpenter, 1857)

in the Shell-Plates of

Acanthochitona hirudiniformis (Sowerby, 1832)

BY

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THE LITHOPHAGES and their coral hosts have been the subject of recent study (KLEEMAN, 1980; MORTON & SCOTT, 1980), and also have been reported from a variety of other, perhaps unusual, hosts including other bivalve shells (HODGKIN, 1962; KEEN, 1971) and chiton shell-plates (BULLOCK & BOSS, 1971). This note reports their occurrence in another unusual host, an acanthochiton.

During a taxonomic investigation of the New World Cryptoplacidae I discovered the presence of *Lithophaga (Leiosolenus) spatiosa* (Carpenter, 1857) in the shell-plates of *Acanthochitona hirudiniformis* (Sowerby, 1832). These specimens, from a lot of 23 from the American Museum of Natural History, lot no. 162150, were collected at Camaron, Panama, by Eugene Bergeron in March of 1969. BULLOCK & BOSS (1971) reported on a similar occurrence involving *Lithophaga (Myoforceps) aristata* (Dillwyn, 1832) in the shell-plates of *Chiton tuberculatus* Linnaeus, 1758, from the Caribbean, and *Chiton stokesii* Broderip, 1832, from the same region of the Eastern Pacific as *A. hirudiniformis* (Sowerby, 1832).

The observations on the three affected examples of *Acanthochitona* generally agree with those of Bullock and

Boss in *Chiton*. The erosion of the shell-plates appears to be a prerequisite for lithophage burrowing as uneroded specimens were not affected. Burrows followed the direction of growth of the shell-plates and destruction involved both the tegmentum and the articulamentum. The formation of an initial burrow appeared to greatly enhance the chances of future infestations by allowing larval lithophages to settle in that burrow. The most heavily affected acanthochiton, 30 mm in length, contained 10 lithophages; the second specimen, 28 mm in length, contained 3 bivalves; the third, 23 mm in length, 1 bivalve. All lithophages were less than 3 mm in length.

Undermining by the bivalves results in a loss of functional esthetes and in greatly weakened shell-plates. Too little is known about the nature of acanthochiton esthetes to determine what type of sensory loss accompanies this burrowing or what effect this has upon the behavior of the chiton. More significant may be the weakening of the shell-plates by the burrows, which in the largest specimen were brittle and fragmented, exposing the chiton's underlying mantle. Obviously the small size of acanthochiton valves cannot support a lithophage to maturity; this unfortunate relationship must be considered detrimental to both lithophage and chiton.

ACKNOWLEDGMENTS

I would like to thank Dr. R. C. Bullock for commenting upon early drafts of this note. The systematic studies of the acanthochitons were supported by a scholarship from the National Capital Shell Club and a Sigma Xi Grant-in-Aid of Research.

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Range Extension of *Kelletia kelletii*

BY

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A SINGLE *Kelletia kelletii* (Forbes, 1852) was collected by the author on 2 May 1980 at the Hopkins Marine Life Refuge, Pacific Grove, Monterey County, California. This specimen (92.1 mm total length; male) was found while using SCUBA at a depth of 10 m in a rocky, *Macrocystis* forest habitat. A second live individual (69.5 mm) was obtained by divers from the same area in June 1980. Two adult-sized *K. kelletii* were collected by SCUBA divers in kelp forests off the mouth of Big Creek along the Big Sur coast, Monterey County in May 1980 (M. G. Kellogg, pers. comm.). Finally, a fifth *K. kelletii* (97.5 mm; male) was found on 19 January 1981 by J. B. Thompson in a Monterey *Macrocystis* forest at a depth of 10 m.

These records are significant due to the lack of reports of *Kelletia kelletii* north of Point Conception (Abbott, 1974; McLean, 1978). The observation of five adult-sized *K. kelletii* in Monterey County suggests that the range of the species should be extended approximately 250 km northward to Monterey, California.

ACKNOWLEDGMENTS

I thank the Hopkins Marine Station for providing diving facilities and C. Baxter and J. Nybakken for confirming the identity of specimens. The first specimen mentioned in this report is preserved in the Moss Landing Marine Laboratories Invertebrate Museum Collection (acc. no. 036).

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A. S. Z.

The 1981 Meeting of the American Society of Zoologists
and

Animal Behavior Society
Crustacean Society
Society of Protozoologists
Society of Systematic Zoology
and American Microscopical Society

at the Hyatt Regency in Dallas Texas

December 27 - 30, 1981

A number of Symposia are already planned and more will be organized in the near future. The meeting is hosted by Southern Methodist University, John L. McCarthy, Chairperson.

For more information, contact Mary Wiley, Business Manager, American Society of Zoologists, Box 2739 Californian Lutheran College, Thousand Oaks, California 91360. Telephone: (805) 492-3585.

Publication Date of THE VELIGER

THE PUBLICATION DATE of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US\$8.00 in all cases

where the Veliger goes to domestic addresses, and a deposit of US\$25.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

We think it important to bring to the notice of all our actual and potential correspondents that the postal fee for registered articles is the highest in the world: \$3.25 regardless of destination. Further, to certain countries it is not possible to have mail pieces insured or registered. In the cases where the prospective recipient desires our communications sent as registered article, we must expect advance payment of that fee. We are unable to return manuscripts (either for reworking or with the recommendation that they be submitted elsewhere) other than by ordinary surface mail. In view of the ever more deteriorating postal services in most countries, we can obviously not assume any responsibility for the safe delivery of any items we must dispatch. Our responsibility must and does end with our delivery to the post office of any item.

Subscription Rates and Membership Dues

We are pleased to announce that at its annual business meeting the Executive Board of our Society has decided to maintain the subscription rate for volume 24 of The Veliger at US\$ 37.50 plus \$1.50 for mailing charges to domestic addresses; however, it is necessary to increase the charge for mailing to all foreign addresses to US\$5.- because the postage rates are scheduled to be doubled in 1981. Also, because many of our subscribers have encountered difficulties in transmitting the necessary funds in Swiss Francs, we have closed our Swiss Postcheck (Giro) account, effective December 31, 1980. Thus, all payments henceforth must be in U. S. funds.

At the same meeting it was also decided to keep the membership dues at the same level as for volume 23, with the mailing charges for domestic addresses at \$1.50 and those for ALL foreign addresses increased to US\$5.-.

Because of some irregularities that have occurred in the recent past, we must stress that membership renewals with the correct amount must reach us on or before April 15 each year; if payment is received after that date, a re-instatement fee of \$1.- is required.

From the foregoing it should be evident that we make a strong effort to combat inflation. But we must ask for cooperation by all our members and subscribers.

Moving?

If your address is changed it will be important to notify us of the new address at least **six weeks** before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. The following charges must be made:

change of address - \$1.-

change of address and re-mailing of a returned issue

- \$2.75 minimum, but not more than actual cost to us.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

At present we are charged a minimum fee of \$15.00 on each order for new addressograph plates. For this reason we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

Sale of C. M. S. Publications:

Effective January 1, 1978, all back volumes still in print, both paper covered and cloth bound, will be available only from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA(alifornia) 93644. The same applies to the supple-

ments still in print with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. West at the address given above.

Volumes 1 through 8 and 10 through 12 are out of print.

Supplements not available from Mr. West are as follows:

Supplements to vol. 7 (Glossary) and 15 (Ovulidae) are sold by 'The Shell Cabinet,' P. O. Box 29, Falls Church, VI(rginia) 22046; supplement to vol. 18 (Chitons) is available from 'The Secretary,' Hopkins Marine Station, Pacific Grove, CA(lifornia) 93950.

Supplements

Supplement to Volume 3:

[Part 1: Opisthobranch Mollusks of California
by Prof. Ernst Marcus;

Part 2: The Anaspidae of California by Prof. R. Beeman,
and The Thecosomata and Gymnosomata of the Cali-
fornia Current by Prof. John A. McGowan]

Supplement to Volume 6: out of print.

Supplement to Volume 7: available again; see announce-
ment elsewhere in this issue.

Supplement to Volume 11:

[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Volume 14:

[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 16:

[The Panamic-Galapagan Epitonidae by Mrs. Helen
DuShane]

[Growth Rates, Depth Preference and Ecological Succes-
sion of Some Sessile Marine Invertebrates in Monterey
Harbor by Dr. E. C. Haderlie]

Supplement to Volume 17: Our stock of this supplement
is exhausted. Copies may be obtained by applying to Dr.
E. C. Haderlie, U. S. Naval Post-Graduate School, Mon-
terey, CA(lifornia) 93940.

WE ARE PLEASED to announce that an agreement has
been entered into by the California Malacozoological
Society, Inc. with Mr. Steven J. Long for the production
and sale of microfiche reproductions of all out-of-print
editions of the publications of the Society. The microfiches
are available as negative films (printed matter ap-
pearing white on black background), 105 mm × 148 mm
and can be supplied immediately. The following is a list
of items now ready:

Volume 1 through Volume 6: \$9.00 each.

Volume 7 through Volume 12: \$12.00 each.

Supplement to Volume 6: \$3.00; to Volume 18: \$6.00

California residents please add the appropriate amount
for sales tax to the prices indicated.

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Avenue, Long Beach, California 90814.

Volumes and Supplements not listed as available in
microfiche form are still available in original edition from
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93644. Orders should be sent directly to Mr. West.

Single Copies of "The Veliger":

We have on hand some individual copies of earlier issues
of our journal and are preparing a list of the various issues
available with the prices. Some issues are present in only
one or two copies, while others may be present in 10 or
more copies. As we are anxious to make room, we will
offer these numbers at an exceptionally low price. This
list may be obtained by sending a self-addressed, stamped
envelope to the Veliger, 1584 Milvia Street, Berkeley,
CA(lifornia) 94709. Foreign correspondents should en-
close one international postal reply coupon. Requests for
the list, for which return postage is not provided, will be
ignored.

Membership open to individuals only - no institutional or
society memberships. Please send for membership ap-
plication forms to the Manager or the Editor.

Membership renewals are due on or before April 15
each year. If renewal payments are made after April 15
but before March 15 of the following year, there will be
a re-instatement fee of \$1.-. Members whose dues pay-
ments (including the re-instatement fee) have not been
received by the latter date, will be dropped from the rolls
of the Society. They may rejoin by paying a new initiation
fee. The volume(s) published during the time a member
was in arrears may be purchased, if still available, at the
regular full volume price plus applicable handling charges.

Backnumbers of the current volume will be mailed to new
subscribers, as well as to those who renew late, on the
first postal working day of the month following receipt of
the remittance. The same policy applies to new members.

THE VELIGER is not available on exchange from the Cali-
fornia Malacozoological Society, Inc. Requests for re-
prints should be addressed directly to the authors con-
cerned. We do not maintain stocks of reprints and also
cannot undertake to forward requests for reprints to the
author(s) concerned.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of \$1.- to a percentage of the value of the draft, going as high as 33%. Therefore we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of First Interstate Bank (formerly United California Bank). This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable except as indicated elsewhere in this section.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of \$4.25 (to reimburse us for the expenses involved in redeeming them) and at \$0.95 per \$1.- face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time, that is 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed \$400.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, \$400.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U. S. A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are submitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript – including figure explanations and the "Literature Cited" section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the "dead letter" office; in other words, it is destroyed.

General Notice

Because of an increasing number of strange occurrences your editor deems it important to clarify our policy with respect to correspondence.

1. We never reply to letters that do not reach us. Since the U. S. postal service no longer forwards mail pieces that are not franked properly, correspondents waiting for our reply might consider the possibility that their letter falls into this category.
2. We do not acknowledge the receipt of a manuscript unless a self-addressed, stamped envelope is enclosed.
3. We do not reply to complaints regarding the non-arrival of our journal, if these complaints are made at a time when the claimed issue could not possibly have reached its destination. In view of the poor postal service throughout the world, it is unrealistic to expect, for example, the July issue in a shorter period than from 2 to 3 weeks in the United States, in less than 4 to 6 weeks in Europe, and in less than 2 to 4 months in other areas of the world; South American countries, in particular, have to expect maximum delays. It should be obvious that we are not responsible for the postal service.
4. We particularly object to complaints about non-receipt of issues which are scheduled to be published as much as 6 months after the complaint was sent! A little consideration of what is possible and what is absurd should help to obviate such untimely complaints.
5. We are receiving an increasing number of requests for our list of individual back numbers that are still available, as well as for our suggestions to prospective authors. These requests state that a self-addressed stamped envelope is enclosed — but somehow the writer must have forgotten to do so. These requests also are not answered by us.

We consider that our policy is justified for several reasons: the requirement for self-addressed, stamped envelopes has been stated in every issue of the Veliger for

the past several years. Since we are a non-profit organization, we prefer to reserve our energy and our resources for productive purposes. However, we do conscientiously, and usually exhaustively, reply to all correspondence that we consider legitimate. Moreover, such correspondence is usually answered the same day as received, with the reply posted the next morning at the main post office in Berkeley. What happens afterwards is beyond our control.

Policy Regarding Reprints

It seems necessary to bring the following points to the notice of prospective authors:

All manuscripts submitted for inclusion in *The Veliger* are subject to review by at least two scientists; acceptance is entirely on the basis of merit of the manuscript. Although many scientific journals assess page charges, the Executive Board of our Society, for the time being at least, wishes to avoid this possible financial handicap to the younger contributors. However, because of the high cost of halftone plates, a suitable contribution to reimburse the Society must be sought.

Similarly, while it was hoped at the "birth" of *The Veliger*, that a modest number of reprints could be supplied to authors free of charge, this has not as yet become possible. We supply reprints at cost. Unfortunately, in recent years it has become "fashionable" for some authors and some institutions to ignore paying for reprints ordered and supplied in good faith or to delay payment for a year or more. This causes financial losses to the Society since our debts are paid promptly. Since the Society is in fact not making any profit, it is necessary to introduce a policy which, it is hoped, will protect us against negligence or possible dishonesty. In the case of manuscripts from sources outside of the United States, if a manuscript is accepted, we will inform the author of the estimated cost of reprints and require a deposit in U. S. funds to cover these costs. If such a deposit is not made, we will not supply any reprints. In the case of non-payment by domestic authors or institutions, we will pursue legal recourses.

BOOKS, PERIODICALS, PAMPHLETS

Nautilus macromphalus in Captivity.

by JECOLN (Japanese Expert Consultation on Living *Nautilus*). Tokai University Press; Tokyo, 1980. xxiv + 80 pp.; numerous ill. Hardbound, \$33.00.

The unusual title and authorship of this book correctly reflect its unusual nature. It consists of a series of 8 reports by 17 Japanese contributors, 11 of whom are members of the Japanese Expert Consultation on Living *Nautilus* (JECOLN). Formation of this group in 1976 was prompted by excitement generated over the arrival of 6 live *Nautilus macromphalus* that had been flown from New Caledonia in July, 1976, to the Yomiuri-Land Marine Aquarium in Tokyo. The goal of the group has been to promote studies of *Nautilus*; this it has done, producing 40 articles between 1976 and 1978 on various aspects of aquarium-maintained *Nautilus*. Unfortunately for many of those interested in the subject, the vast majority of these articles were published in Japanese, in journals that are not readily accessible. While some of the articles consist only of observations and announcements for the layman, a number of them contain new information concerning *Nautilus* that is of interest to both neontologists and paleontologists.

The JECOLN book is primarily a review, in English, of the group's earlier contributions, and as such it is particularly welcome to cephalopod specialists. Included are articles describing living *Nautilus* (T. Habe), aquarium maintenance of *Nautilus macromphalus* (N. Kawamoto and others), observations on behavior and morphology (S. Mikami and others), SEM-based observations of tentacles and mouth parts (Y. Fukuda), shell biometrics (H. Hirano and others), speculations on ecology (T. Hamada & Mikami), and species distribution (T. Hamada). There is a detailed bibliography through 1977, with an addendum of 44 1978-1979 citations. A significant attraction is the 15 pages of color photographs showing many aspects of *Nautilus* activity (feeding, swimming, copulation, egg secretion), soft part morphology and histology. While they do not match the esthetic splendor of Douglas Faulkner's portraits of Palauan *Nautilus* published in Audubon, Smithsonian and National Geographic magazines, the JECOLN pictures do provide scientifically important views of morphology and behavior that are not available elsewhere. The quality of printing, color reproduction and binding is excellent.

Shortcomings of this book include numerous grammatical errors (*e.g.*, sea water is passed through the gills, p. 2) due to translational difficulties, which can be overlooked in return for having the translated version published. Figure mis-numbering (p. xi, figs. 22, 23) is more serious, for in this instance it transposes the sexual identity of specimens illustrating important sex organs and will confuse or even mislead readers who are unfamiliar with *Nautilus*. Some misinformation is presented; the male's spadix is not located ventrally to the buccal mass as stated (p. 2), but is either on the left or right side of the mouth accounting for the greater shell width of males versus females (the latter have no spadix and so their buccal mass is centrally located). A series of full-page maps purports to show the distribution of species of *Nautilus*, including drifted shells and living specimens of *N. scrobiculatus* (fig. 7-1), *N. repertus* and *N. alumnus* (fig. 7-2) and *N. stenomphalus* (fig. 7-3). In fact, however, **none** of these is known from living specimens; with the exception of a single, partly decayed specimen of *N. scrobiculatus* picked up near Milne Bay, New Guinea, by Arthur Willey (1899, 1902), all of these forms are known only from their drifted shells and lack of knowledge concerning living animals has seriously inhibited understanding species distinctions and distribution of *Nautilus*. JECOLN has placed considerable emphasis on establishing—and subsequently breaking—longevity records for aquarium-maintained *Nautilus* (9 months, p. 4). However, if records are to be recognized, first prize should go to Bruce Carlson and his associates at Waikiki Aquarium, who have kept a specimen of *N. macromphalus* alive for almost 2 years, and second prize to Claude Spinoso who has maintained several Palauan *Nautilus* in a home-built system, at Boise State University, for over a year. This aquarium aspect of *Nautilus*, which is the central theme of JECOLN's book, bears emphasizing; the relative ease with which *Nautilus* can be kept in aquaria, plus the recent availability through dealers of live animals from the Philippines, points to the excellent potential for landlocked, laboratory-based studies and even for keeping *Nautilus* in classroom aquaria for demonstration purposes. Sir Richard Owen (1832), who dissected and described the first animal known to science, would be amazed!

Considering the price of the book, its relative brevity and specialized subject matter, the obvious question is whether its purchase is to be recommended. For the private library of serious *Nautilus* or cephalopod enthusiasts, yes; however, in my opinion, its greatest value will be as a library reference for class or research use. It brings up to date the still-excellent general account of

Nautilus by H. B. Stenzel (1964) and provides a hitherto unavailable pictorial record of the inhabitant of that striking chambered shell. I congratulate JECOLN for their pioneering effort and hope that they continue their efforts in studying and documenting this intriguing, poorly known animal.

Literature Cited

- OWEN, R.
1832. Memoir on the pearly nautilus (*Nautilus pompilius*, Linn.) with illustrations of its external form and internal structure. Council of the Royal College of Surgeons. Richard Taylor, London, 68 pp.; 8 pls.
- STENZEL, H. B.
1964. Living *Nautilus*. pp. K59-K93, in *Treatise on Invertebrate Paleontology* (Part K). Geol. Soc. America and Univ. Kansas Press, Lawrence, Kansas
- WILLEY, A.
1899. General account of a zoological expedition to the South Seas during the years 1894-1897. Proc. Zool. Soc. London for 1899: 7-9 (June 1899)
1902. Contribution to the natural history of the pearly nautilus. Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896 and 1897. Part 6: 691-830; pls. 75-83. Cambridge Univ. Press; Cambridge, England

W. Bruce Saunders,
Department of Geology
Bryn Mawr College

Guide to the Nudibranchs of California

by GARY R. McDONALD & JAMES W. NYBAKKEN. 1980. 72 pp. 111 col. figs. + 1 b&w fig. on 14 pls.; 36 text figs. 21.5 × 28 cm, paperbound. American Malacologists, Box 2255, Melbourne, FL 32901. \$13.50

This is a most usable and accurate account on the nudibranchs of California. The introductory material is clear and well prepared. The table of food preferences is an important addition, although one wishes that the phyla of the items listed had also been given.

The colored illustrations (8 to a page) do not do justice to the original photographs because the registry of a number of the plates is off (the individual illustrations are generously advertised as "plates"). On the other hand, the cover design is outstanding.

The dichotomous keys seem clear and workable. The basic text for each species includes a good description, as well as notes on distribution, habitat, and nomenclature. One wishes that the taxonomic discussions had been a little more thorough to explain the decisions about syn-

onymies and to give more uniformly the original combinations of the species.

On the whole, however, this is a book we can recommend for students of the molluscan fauna of California:

Eugene V. Coan

Prevention and Removal of Fouling on Cultured Oysters A Handbook for Growers

by KOHMAN Y. ARAKAWA, translated by REGINALD B. GILLMOR. 38 pp.; 20 figs. in text. Maine Sea Grant Technical Report 56; Ira C. Darling Center, University of Maine at Orono, Maine 04573. 1980.

Although the publication is based on work done in Japan, its findings are applicable wherever oysters are cultivated, or, in fact, wherever fouling in marine environments is of importance. A bibliography of about 90 titles will be a welcome guide to some of the more important publications pertinent to the central problem.

R. Stohler

Genera of the Bivalvia A Systematic and Bibliographic Catalogue (Revised and Updated)

by HAROLD E. VOKES. Paleontological Research Institution, Ithaca, New York, N. Y. 14850. xxvii + 305 pp. Available from Paleontological Research Institution at \$20.00 plus postage and handling (although a flyer lists this latter charge at \$1.81, your reviewer doubts that this amount is sufficient in the face of recent large increases in U. S. postage rates).

This revised and updated revision of Vokes original "Genera of Bivalvia" is of great importance for all serious workers in the field of bivalves, be they concerned with physiology, anatomy, or whatever other topic; the taxonomist will find it an absolute must for his working library. We wish to stress the need by the non-taxonomist for this work as it is too frequently overlooked how important a correct citation of the name of a research subject is; incorrect names (not necessarily synonyms, but actually wrong names) make the proffered work valueless.

The price of the book, in today's market, is rather modest.

R. Stohler

After our April issue had been published, we received a letter from Mr. Poorman stating in part: "... there is one problem with figs. 11 and 13 in the new species. The text is correct and the captions; but the radular drawings have been exchanged. ..." He further indicated that the error occurred when the final mock-up was prepared.

We therefore present herewith, together with Mr. Poorman's apologies, new copies of the same drawings with correct figure numbers and the suggestion that the drawings be pasted in the correct place on pp. 341 and 342, respectively. Please avoid the use of rubber cement!

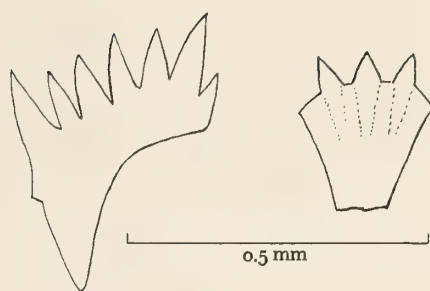


Figure 11

Radula of *Fusinus humboldti* Poorman, spec. nov.
 $\times 100$

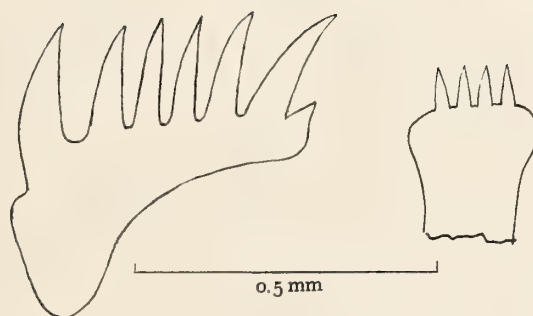


Figure 13

Radula of *Fusinus paulus* Poorman, spec. nov.
 $\times 100$

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in **THE VELIGER** is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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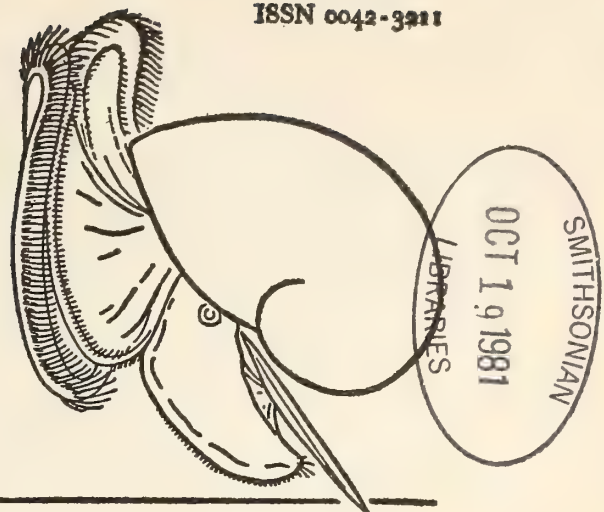
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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, Genus, (Subgenus)
New Taxa

A Method for Artificially Protracting Gastropod Radulae and a New Model of Radula Function

BY

TOM E. MORRIS¹ AND CAROLE S. HICKMAN

Department of Paleontology, University of California, Berkeley, California 94720

(1 Plate; 2 Text figures)

INTRODUCTION

MANY DISTINCT ASPECTS of the mechanical and ecological function of gastropod radulae can be inferred from morphology alone (HICKMAN, 1977, 1979a, 1979b, 1980). However, understanding the integrated function of the entire apparatus requires some knowledge of the relationship of the radula to the underlying odontophoral cartilage (MORRIS, 1980). We describe here a method of artificially protracting the odontophore and radula from the mouth of a freshly anesthetized specimen for observation of teeth in functional configuration. The artificial protraction compares closely in detail with still photographic and slow-motion microcinematographic representations of radular action in living snails and provides new data on radular movement patterns.

General models of radular function depict the radula as a flat, toothed belt or ribbon that is manipulated over the end of the odontophore, which is customarily illustrated as or conceptually simplified to a pulley (ANKEL, 1938: fig. 16, p. 238), a straight-edged plane (MÄRKEL, 1964; NISBET, 1973: fig. 9, p. 446; SOLEM, 1974) or a plane with a central notch or "Knickstelle" (EIGENBRODT, 1941).

The actual situation is much more complex, however, and RUNHAM (1969) urged that radulae be viewed while still in contact with the subradular membrane and odontophore. He illustrated the radulae of species of *Agriolimax* and *Nucella* on excised odontophores dissected from the buccal mass, quick-frozen, and freeze-dried. However, this method does not provide information about radular

configuration under tension during feeding or data on tooth and row movements.

MATERIALS AND METHODS

Specimens of the common eastern Pacific intertidal trochid gastropod *Tegula funebris* (A. Adams, 1854) were anesthetized for at least 24 hours in a solution of 7% magnesium chloride in an equal volume of seawater at 7°C. Osmolality was adjusted with tapwater or synthetic sea salt to approximately 970 mOs/kg, close to that for seawater, and pH was adjusted with 1N hydrochloric acid or 1N sodium hydroxide to u.2. Gradual addition of the anesthetic prevented retraction of the animals.

Relaxed animals were removed from cracked shells and the visceral mass, and operculum were trimmed as illustrated in Figure 1A. The animal was then placed upon its dorsum and pinned to a wax-bottom dissecting tray under seawater. Next, 3 to 5 loops of sewing thread were placed around the animal as illustrated in Figure 1B. The loops were then tightened from posterior to anterior. Tightening produces an artificial peristalsis, and the horns of the odontophore are protruded from the mouth. If the cartilages protrude symmetrically (sometimes they do not), the subradular membrane is then carefully "walked" around the cartilage tips with forceps (Figure 1C) until the radula itself can be grasped. The tip of the radula is then pulled slightly out of the mouth, over and around the cartilages.

Tension placed upon the radula will pull it between the cartilages, maintaining an enrollment of the posterior portion of the radula where it disappears into the mouth. At the same time, the anterior portion will flatten out and remain flat as it is pulled anteriorly around the cartilages.

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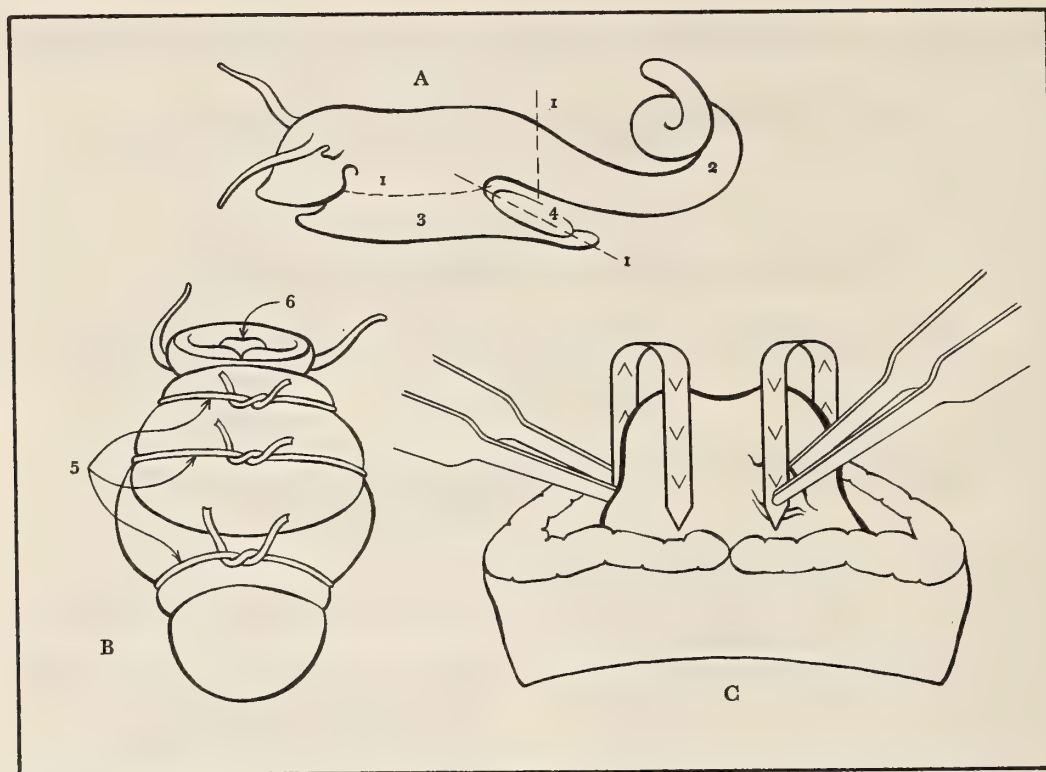


Figure 1

Steps in artificial protraction of a gastropod radula
 A. animal, removed from its shell, showing the trim lines (1) for removing the viscera (2), foot (3), and operculum (4). B. trimmed animal on its dorsum, showing the threads (5) used for artificial

peristalsis and the protruded odontophore (6). C. detail of the protruded odontophore illustrating the way forceps are used to pull the subradula membrane and radula around the tips of the cartilages.

Explanation of Figures 2 to 9

Figure 2: Artificially protracted radula of *Tegula funebris*, oriented as in the diagrammatic representation in Figure 1C

Bar = 1 mm

Figure 3: Detail of the protraction in Figure 2, showing the tight posterior enrollment of the radula as it disappears into the mouth

Bar = 400 μ m

Figure 4: Optical micrograph of living *Tegula funebris* with its radula protracted against an aquarium wall, from a 35 mm negative

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Figure 5: Optical micrograph of living *Tegula funebris* from a 16 mm frame of a slow-motion movie film of feeding strokes on an aquarium wall

Bar = 1 mm

Figure 6: Detail from an artificial protraction illustrating the manner in which the tops of cusps overlap to form a series of function-

ally integrated units of gradational inferred ability to sweep up increasingly finer particles as they pass sequentially over an area of substrate

Bar = 200 μ m

Figure 7: Detail from the same area of the radula illustrated in Figure 6 rotated and tilted to show the way that cusp tops and inner edges are presented to the substrate and the manner in which food (at arrows) can be trapped in the grooves beneath the cusps

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Figure 8: Detail of the food collecting groove along a portion of a marginal tooth row

Bar = 50 μ m

Figure 9: Simulated operational configuration of an excised radula of *Tegula funebris*, manipulated to approximate the relationships observed in the artificial protraction and in living snails

Bar = 400 μ m

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*Original
fig. 1*

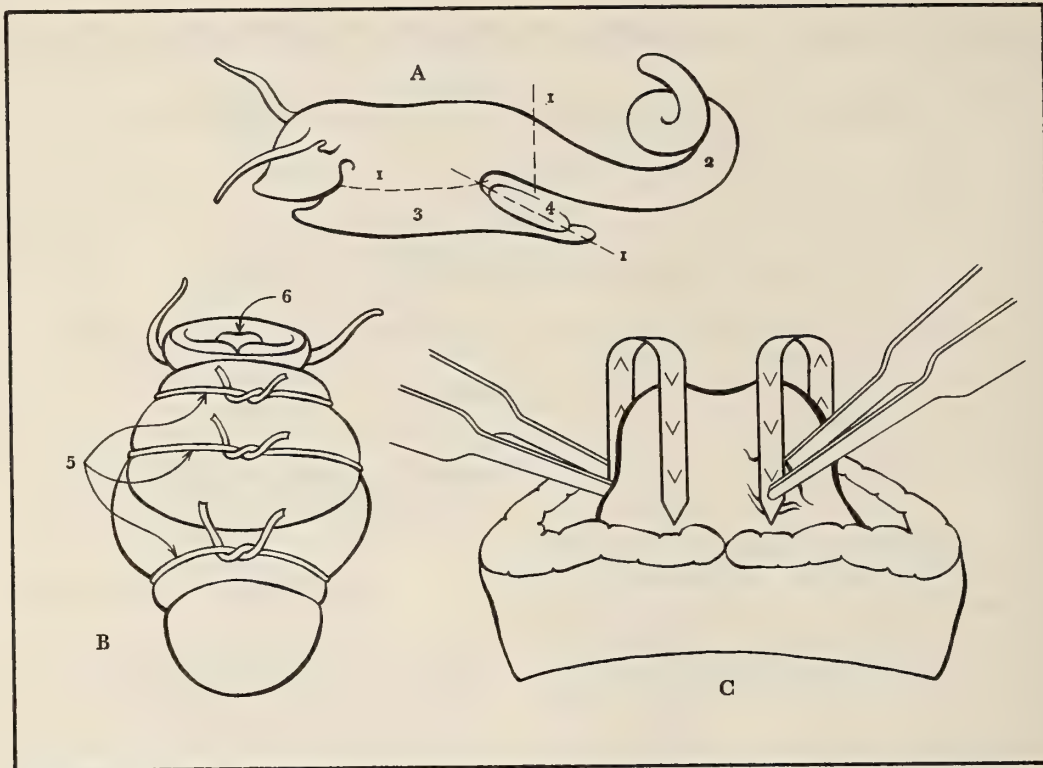


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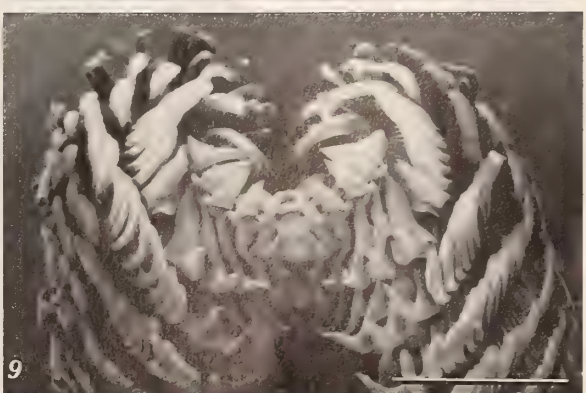
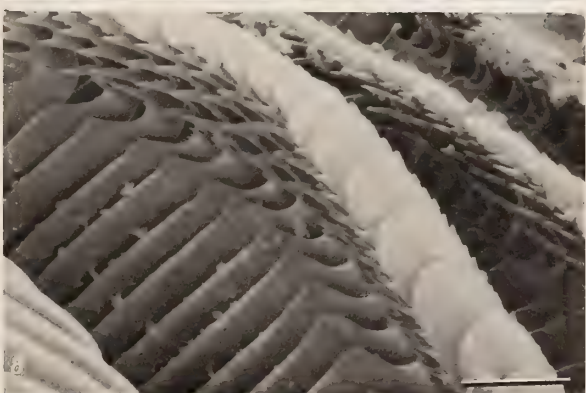
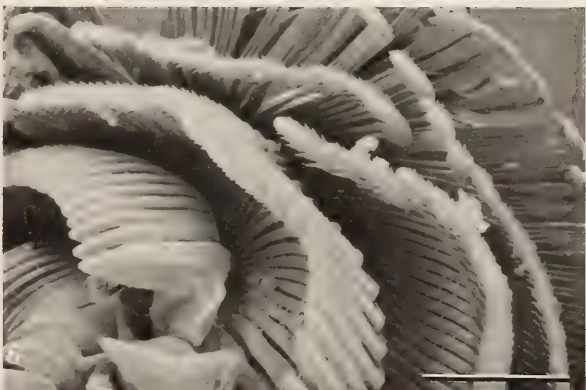
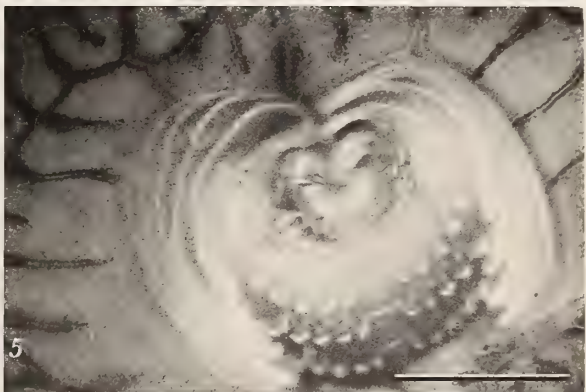
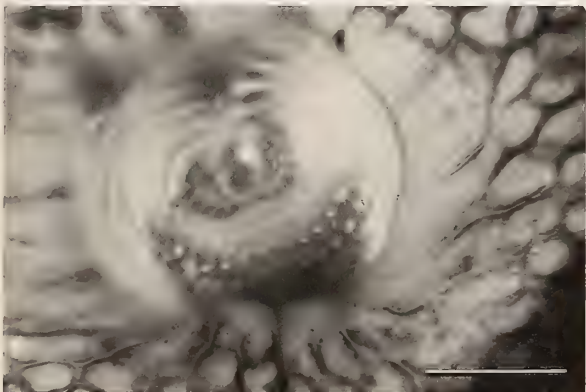
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Bar = 50 μ m

Figure 9: Simulated operational configuration of an excised radula of *Tegula funebris*, manipulated to approximate the relationships observed in the artificial protraction and in living snails

Bar = 400 μ m



The resulting conformation (Figures 2 and 3) is very similar to the shape of the radula photographed during the feeding of live animals (Figures 4 and 5).

When a satisfactory protraction has been achieved, the radula is held in place, under seawater, by one pair of forceps while with the other hand fixative is applied to the preparation with a hypodermic syringe and needle. Several fixation techniques were attempted, including double fixation with glutaraldehyde and osmium tetroxide. However, the best results were obtained with a single fixation in 4.7% formalin (100 mL 36% formaldehyde + 260 mL synthetic seawater + 400 mL tapwater) at pH 7.2 and 970 mOs/kg. After several minutes of initial hardening, the seawater was drained and the dissection immersed in the fixative, covered, for 8 hours.

The fixed preparation is finally trimmed, dehydrated through an ethanol series, critical point dried, dipped in a room-temperature solution of 0.25% formvar in an ethylene dichloride solvent (see PEASE & BAILEY, 1975), a polymer that helps reduce charging during SEM viewing, and coated with gold or gold palladium immediately prior to viewing.

RESULTS

Artificial protractions obtained by the methods outlined above demonstrate an interesting relationship between the radula and the underlying odontophoral cartilages. The relationship differs significantly from the standard model of radular motion that visualizes the radula as a flat, toothed ribbon operated over a straight-edged or terminally notched bending plane. The protraction illustrated in Figures 2 and 3 clearly shows that the posterior portion of the radula is tightly enroled rather than flat as the radula emerges from the buccal cavity and as it is withdrawn again. As a consequence the anterior portion of the radula is drawn into a shape that arrays teeth in a tight semicircular configuration during feeding.

This same configuration is confirmed by means of still micrography (Figure 4) and slow-motion microcinematography (Figure 5) of live snails feeding on a glass aquarium wall. Microcinematography, in fact, provides the essential tool for tracing the paths of teeth and tooth rows during the feeding stroke and for understanding the detailed sequence of events that occurs very rapidly during the feeding stroke. The results of frame-by-frame analysis of radular action in *Tegula funebris* will be treated in a separate paper.

Still micrography and microcinematography are inadequate for resolving details of morphology because of the narrow depth of focus in a highly three-dimensional dynamic biomechanical apparatus. The artificial protraction is therefore important because it retains the details of relationships between tooth shafts, cusps, and bases for elucidation with scanning electron microscopy (HICKMAN, 1977). Figures 6-8 illustrate a few of the relationships that are particularly important in understanding how food is prepared and gathered.

The overlapping cusps and inward rotation of the longitudinal axis of cusp tops, both within rows as they approach the inner radular fold and across a posterior to anterior transect of successive rows (Figure 6) suggest a path of movement of functionally interactive units that is confirmed and elucidated in detail through microcinematographic frame-by-frame analysis (MORRIS, 1980; MORRIS & HICKMAN, in prep.).

Rotation of the same protraction (Figure 7) provides a different perspective on cusp interaction, demonstrating the manner in which cusp tops and inner edges are presented as a unit to the substrate surface. Note at the arrows in Figure 7 the manner in which material from the substrate has collected beneath a portion of the inferred scraping edge.

With additional specimen rotation and higher magnification (Figure 8) the detailed morphology of what we interpret as a "food collecting groove" is revealed between tooth cusps and shafts. All of these fine morphological details become important in analysis of paths and sequences of tooth and row motions so elegantly revealed through microcinematography.

These results indicate that simulations of operational configuration cannot be obtained by simply folding the radula, as assumed in the "belt-and-pulley" model of radular function (HICKMAN, 1980: fig. 1c). It is, however, possible to manipulate an excised radula, once it has been separated from the odontophore and subradular membrane, into roughly functional configuration by enrolling the posterior portion of the radula as tightly as possible after folding. The simulation illustrated in Figure 9 is roughly comparable to the configurations produced by artificial protraction and those observed in living snails during feeding. However, the simulation does not offer the same refinement of detail of tooth interactions as the artificial protraction, particularly with respect to the orientation of cusps as compound food preparation and gathering devices.

CYLINDER MODEL OF RADULA FUNCTION

While developing the artificial protraction method and manipulating the radula under tension over the horns of the odontophore, it became clear that the simplistic model of radular action involving a straight-edged bending plane and flat radula is conceptually inaccurate for the rhipidoglossate radula. We replace the old model with a cylinder model that is not much more difficult conceptually and that sets the stage for an accurate and more dynamic understanding of the way food is prepared and gathered.

The key to understanding the new model follows from recognition that the posterior portion of the radula is tightly enrolled rather than flat as the radula is protracted and retracted.

Protraction of the radula is initiated by the radula tensor muscles, which pull the subradular membrane and radula forward and down between the cartilages. Retention of the cylindrical configuration is encouraged by the narrow space that the radula must occupy between the tips of the cartilages. This configuration is also a partial reflection of the shape of the radula as it is stored in the radula sac, which acts as a folding template. As the anterior portion of the radula moves farther forward and over the ends or horns of the odontophore, the ribbon is flattened as it moves up into the sublingual pouch.

To visualize how these events occur, let us first consider the radula as an elongate, flat, elastic ribbon, anterior end down, with solid lines representing tooth rows (Figure 10A). When the distal margins of the ribbon are brought together evenly above the surface occupied by the teeth, a cylinder is formed (Figure 10B). This represents the

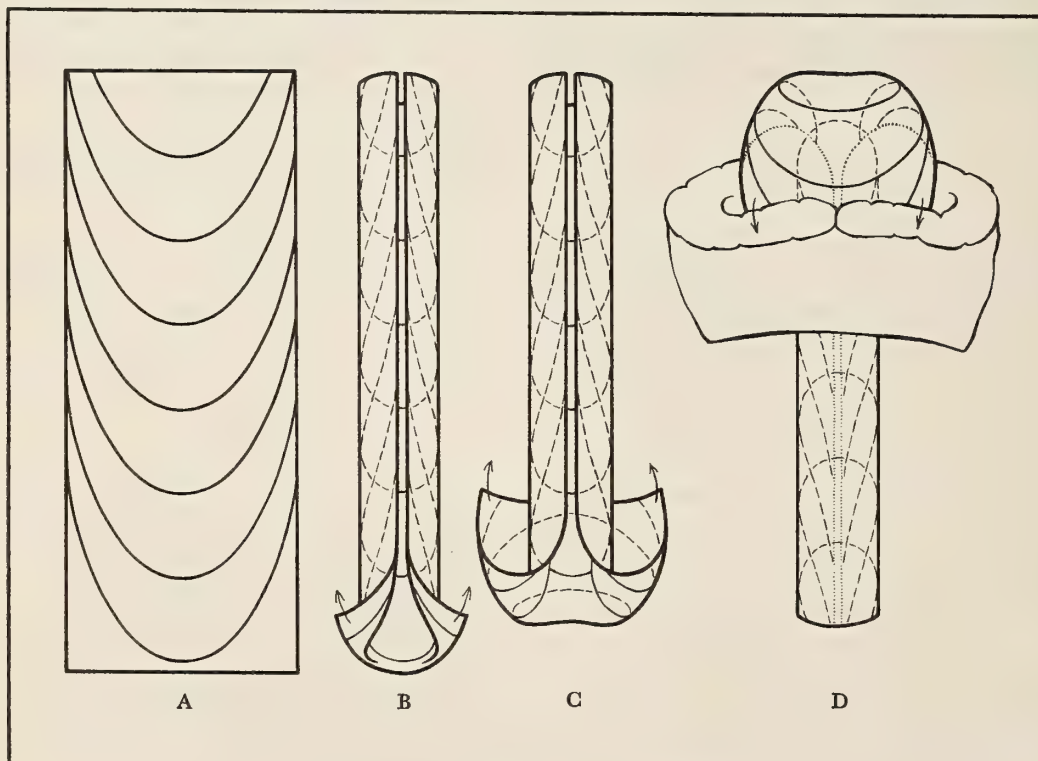


Figure 10

The cylinder model of radula function

A. flat, flexible strip representing radula, with curved lines indicating tooth rows. B. flexible strip rolled into a cylinder, with dashed lines representing the geometry of tooth rows inside the cylinder. C. Cylinder with corners pulled back as indicated by arrows, pro-

ducing semicircular crease anteriorly while remaining enrolled posteriorly. D. Cylinder model reoriented and placed diagrammatically in gastropod mouth for comparison with artificial and natural protractions.

actual form assumed by the radula in the radula sac and the form that is preserved under tension between the horns of the odontophoral cartilage during protraction.

To visualize what happens to this cylindrical configuration as the radula moves over the tips of the cartilage and into the sublingual pouch, we pull the corners of the anterior edges of the cylinder back and away from the meeting edge (Figure 10B). As we continue to draw the edges back (Figure 10C), the anterior section of the band unfolds and flattens at a right angle to the cylinder. The posterior integrity of the cylinder remains, while the area of transition to flat band is marked by a semicircular crease. It is at this semicircular crease (the "Knickstelle" of EIGENBRODT, 1941) that the radula contacts the substrate. The main food-gathering action of the radula occurs as the crease moves anteriorly up the band during retraction, so that successively more anterior rows of teeth fold inward and assume a progressively tighter semicircular configuration before disappearing into the mouth. Figure 10D illustrates the fully protracted cylinder model in the context of the mouth, oriented for comparison with illustrations of full artificial protraction (Figures 1C and 2).

DISCUSSION

Although the method described above is applicable to other gastropods, we expect that protractions of species with fundamentally different radular morphologies and odontophore shapes will reveal somewhat different functional configurations. These configurations should suggest alternative operational modes of food preparation and food gathering. We are not certain how broadly applicable the cylinder model of radular function will prove to be. Some radulae, even within the family Trochidae, cannot be made to assume a cylindrical shape comparable to that of *Tegula funebris*. For example, in the typical radula characterizing trochids of the subfamily Solariellinae (HICKMAN, 1977, 1980), the flat, blade-like marginal teeth fold over the rachidian and lateral teeth along a sharp, localized hinge so that the collapsed radula is flat rather than enrolled. We predict a different mode of operation for the solarielline radula. Experimentation with other species is encouraged.

CONCLUSIONS

Artificial protraction of gastropod radulae provides an accurate representation of the configuration of teeth relative to the underlying odontophore while the radula is under tension. Behavior of the radula of *Tegula funebris* during artificial protraction bears little similarity mechanically to a belt and pulley. A cylinder model best explains radula function: the radula behaves as a flat band anteriorly and a slit flexible cylinder posteriorly, with a movable semicircular crease at the region of transition controlling tooth positions and movements during feeding. Experimentation with other species is required to determine the range of mechanical repertoires that have evolved within the Gastropoda.

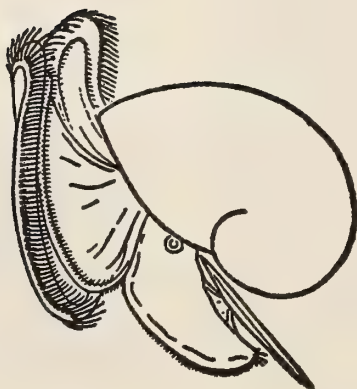
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Crystalline Style Cycling in *Ilyanassa obsoleta* (Say)

(Mollusca : Neogastropoda);

Further Studies

BY

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(1 Text figure)

INTRODUCTION

Ilyanassa obsoleta is unusual among neogastropod snails in that it possesses a true crystalline style (NOGUCHI, 1921; JENNER, 1956; BROWN, 1969). It has been suggested that the style of *I. obsoleta* is necessary as an adaptation for digesting plant starches in the diet (JENNER, 1956; SCHELTEMA, 1964; BROWN, 1969). Work of WETZEL (1977) and of HAINES & MONTAGUE (1979) indicate that most of this snail's carbon comes from benthic diatoms, which lends support to the notion that the style is a key adaptation for nutrient procurement. CURTIS (1980) has described the results of five studies, carried out in 1978 on the Cape Henlopen sandflat near the mouth of Delaware Bay, which were undertaken in an attempt to determine the temporal occurrence of crystalline styles among snails in this population. It was found that snails tended not to have styles shortly after dawn regardless of tidal stage, indicating a daily pattern of waxing and waning. CURTIS & HURD (1980) have shown that reduced salinity also brings about style loss in *I. obsoleta*.

It is our purpose here to provide new information which adds to our general understanding of the crystalline style cycle in *Ilyanassa obsoleta* in natural habitats. New evidence reported here comes from six additional style cycle studies, carried out in 1979, designed to determine: 1) if the pattern observed in 1978 was evident during a second year at the same study site, and 2) if the style behaved in a nearby salt marsh habitat as it did on the sandflat. In addition we used a binomial distribution to develop a statistical criterion to identify general style loss events in the Henlopen population.

MATERIALS AND METHODS

Study Site

The general study area is located just inside the mouth of Delaware Bay, on the western shore (75°06' W; 38°47' N). Two habitats were selected for study from within this area, a sandflat and a ditched *Spartina* salt marsh.

The sandflat population of *Ilyanassa obsoleta* inhabits a band along the shore of approximately 1500 m long by 100 m wide. Snails are not found subtidally in this habitat, but may reach densities as high as 1 000/m² in the intertidal region. Sediments on the sandflat consist primarily of fine to medium sand. Tidal range is 1 - 1.5 m, and salinity is normally 25 - 30‰, but may drop to 10‰ upon the occasion of heavy rain at low tide. Snails were sampled in this habitat from just below MLW in a zone of high snail abundance.

The 200 ha Canary Creek salt marsh habitat is located approximately 5 km WNW from the sandflat. The two populations are discontinuous. Drainage of the high marsh portion of this habitat is provided by a series of parallel mosquito ditches, which connect to a central tidal creek. The marsh therefore represents a more convoluted and spatially heterogeneous habitat than the sandflat. Snails are found chiefly in the mosquito ditches, which are above MLW and therefore intertidal. Two sample sites for snails were chosen, one at the juncture of a mosquito ditch and the main tidal creek (mouth-of-ditch site), and the other approximately 300 m up an adjacent ditch (high-marsh-ditch site). Sediment at the former site was heavy black mud and at the latter consisted of scoured sand.

Procedures

Studies reported upon here were conducted essentially as were those described by CURTIS (1980). Samples of ten snails (16-25 mm shell height) were collected hourly from the chosen site(s) and returned to the laboratory where observations were made on shell height, sex, condition of crystalline style, type of material in the gut, and incidence of parasitism. In the field at each collection, observations on water depth, temperature and salinity were made. Observations other than on crystalline styles will be discussed elsewhere. All 1979 studies lasted for either 27 or 28 consecutive hours.

Studies were conducted simultaneously at the sandflat and high-marsh-ditch sites on two occasions to compare features of the style cycle between these habitats. Since both solar and tidal phenomena affect the style cycle (CURTIS, 1980), these were timed so that dawn coincided with low tide during one study, and high tide during the other. In addition, two separate studies were carried out with the same considerations for dawn and tidal stage at the mouth-of-ditch site, for the purpose of examining within-habitat variation in style cycle in the physically heterogeneous marsh.

We used a negative binomial probability distribution (SOKAL & ROHLF, 1969) to determine expected probabilities of style occurrence among samples of ten snails. These probabilities allow us to analyze samples to distinguish nonrandom style loss events in the population from chance occurrence.

RESULTS

Table 1 summarizes data from the 1978 and 1979 studies. Overall probability of a snail having a style in each of the eleven studies is shown in this table. Probability of finding a snail with a crystalline style in the Henlopen population is $62 \pm 4\%$, and is consistent between years. This is similar to the probability of style occurrence at the mouth-of-ditch site in the marsh ($65 \pm 6\%$), but is lower than for the high-marsh-ditch site ($75.0 \pm 0.1\%$).

In order to quantitatively interpret data such as those presented in Figure 1 and in CURTIS (1980), it was necessary to develop a statistical criterion to distinguish significant style loss in our population from random variation in samples of ten snails. This involved calculating the probabilities of finding 10/10, 9/10, 8/10 . . . 0/10 snails

Table 1

Numbers and percentages of *Ilyanassa obsoleta* with and without styles collected during Cape Henlopen and Canary Creek, Delaware style cycle studies, 1978 and 1979.

Study date + location	No. + % with styles		No. + % without styles		Total snails
11 July '78	102	57%	78	43%	180
25-26 July '78	155	57	115	43	270
1-2 Aug. '78	149	62	91	38	240
4 Aug. '78	114	63	66	37	180
15-16 Aug. '78	156	68	74	32	230
15-16 June '79	173	62	107	38	280
21-22 June '79	173	64	97	36	270
Mean % Henlopen	$62 \pm 4\%$		$38 \pm 4\%$		1650
15-16 June '79	213	76	67	24	280
21-22 June '79	208	75	71	25	279
Mean % high marsh ditch site	$75 \pm 0.1\%$		$25 \pm 0.1\%$		559
7-8 July '79	197	70	83	30	280
27-28 July '79	169	61	109	39	278
Mean % mouth-of- ditch site marsh	$65 \pm 6\%$		$35 \pm 6\%$		558

with styles present. For this calculation, we used only the seven Henlopen studies (Table 1), since our data pool for this population is both large and consistent, whereas neither can necessarily be said of the marsh snails. Therefore, the probabilities derived can legitimately be applied only to snails from the sandflat.

These probabilities were calculated by expansion of the binomial expression $(p+q)^k$, where p , the probability of having a style = 0.62 (from Table 1); q , the probability of not having a style = 0.38; and k , the sample size = 10 snails. Expected frequencies of each possible outcome of style occurrence in samples of ten snails are given in Table 2, which follows the format of SOKAL & ROHLF (1969). Calculations are based on a total of 1650 snails from all seven Henlopen studies.

Comparison of observed and expected frequencies in this table shows that the snails are not behaving (with respect to style occurrence) as a binomial population. This is so primarily because there are more samples than expected with 10/10 and 9/10 snails having styles, and also more samples than expected in which 3/10, 2/10, 1/10

and 0/10 snails have styles. According to the calculated relative expected frequencies, the probability of randomly collecting a sample of 10 snails in which only three possess styles is approximately 0.03. Since the probability of finding 3/10 or fewer with styles by chance alone is less than 0.05, we have taken this as a criterion for style loss in the Henlopen sandflat population. Based upon this criterion, the chi-square analysis at the end of Table 2 indicates significant style loss in the population for 30 samples in the seven studies, which is considerably more frequent than predicted by chance alone.

Results of the six 1979 style cycle studies are graphically presented in Figure 1. A similar presentation of the five 1978 studies is given by CURTIS (1980). The pattern of style occurrence found in the Henlopen sandflat studies (Figures 1a and b) is similar to that found in the mouth-of-ditch studies (Figures 1e and f), especially with respect to the general co-occurrence of dawn and style loss. In fact, style loss can be seen in seven of the eight dawn periods sampled during these four studies. There is, however, no readily evident pattern to style occurrence in the

Table 2

Expected sample ratio frequencies for the Henlopen sandflat *Ilyanassa obsoleta* population as predicted from the expansion of the binomial expression $(p+q)^k$, where p = the probability of having a style, and q = the probability of not having a style. Based on 165 samples of 10(= k) snails each.

Sample ratio (# styles /10 snails)	Powers of p (= 0.62)	Powers of q (= 0.38)	Binomial coefficients	Relative expected freq.	Absolute expected freq. ($x/165$)	Obs. freq. ($x/165$)
10	0.00839	1.00000	1	0.00839	1.4	11
9	0.01354	0.38000	10	0.05145	8.5	25
8	0.02183	0.14440	45	0.14185	23.4	32
7	0.03522	0.05487	120	0.23190	38.3	18
6	0.05680	0.02085	210	0.24872	41.0	16
5	0.09161	0.00792	252	0.18284	30.2	22
4	0.14776	0.00301	210	0.09343	15.4	11
3	0.23833	0.00114	120	0.03272	5.4	10
2	0.38440	0.00043	45	0.00744	1.2	8
1	0.62000	0.00017	10	0.00105	0.1	8
0	1.00000	0.00006	1	0.00006	0.0	4

Chi-square comparison of observed and expected sample ratio frequencies.

Observational class (# styles/10 snails)	0-3	4	5	6	7	8	9-10
Observed	30	11	22	16	18	32	36
Expected	7	15	30	41	38	23	10

$\chi^2 = 133.7$, d.o.f. = 6, $P < 0.001$.

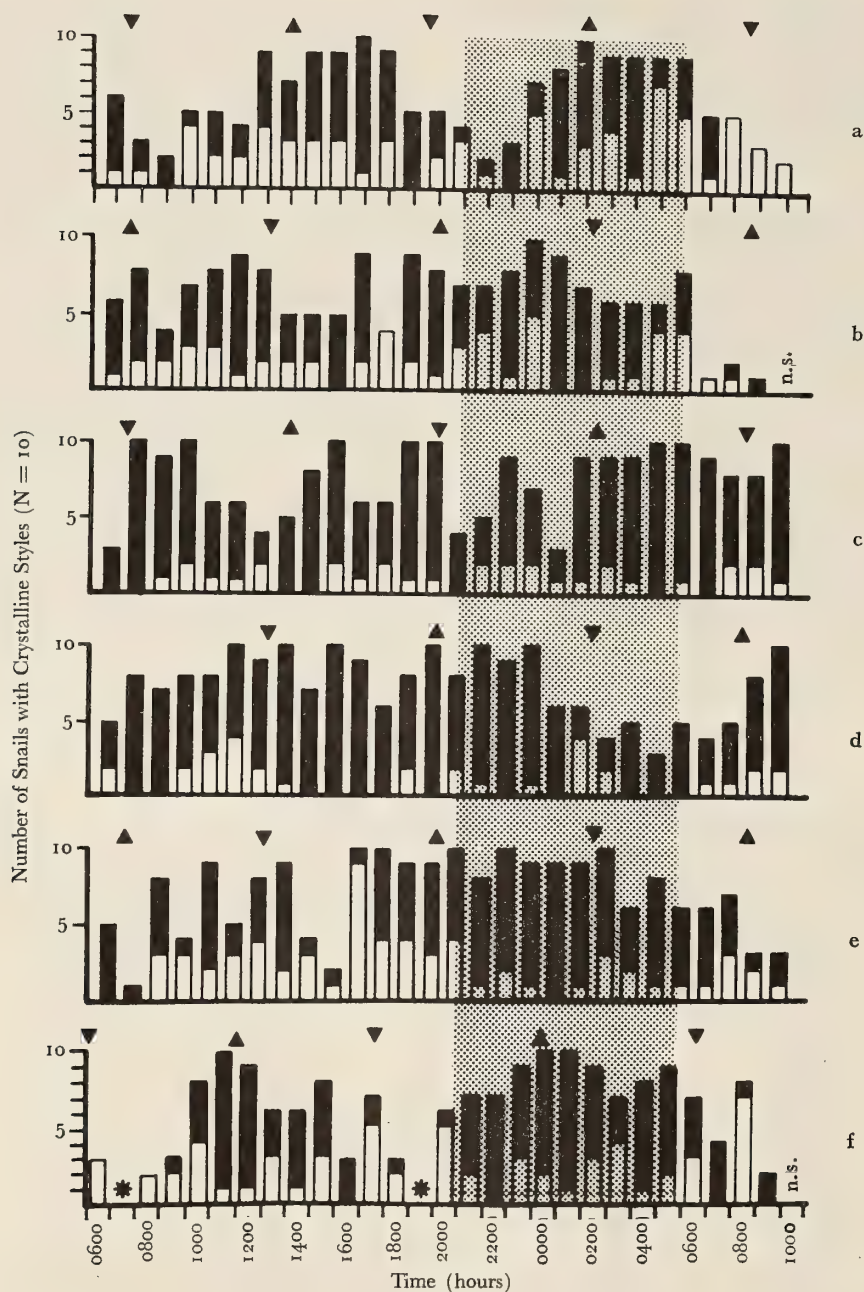


Figure 1

Pattern of occurrence of crystalline styles in *Ilyanassa obsoleta* collected from Cape Henlopen sandflat (a, b) and Canary Creek salt marsh (c, d, e, f), Delaware, summer 1979. Sample sites for c and d, and e and f were different (see text). Studies a and c were carried out on 15-16 June; b and d, 21-22 June; e, 7-8 July; and f, 27-28 July. Height of bars indicates the number of

snails out of 10 which possessed styles; shaded portion of bar indicates fully formed styles, unshaded portion indicates partially formed styles (*i. e.*, waxing or waning); pointers indicate tidal stage (up = high, down = low); asterisks denote complete absence of styles in samples; N.S. indicates no sample taken

Table 3

The relationship of solar and tidal factors (singly and in concert) to style loss events in the *Ilyanassa obsoleta* population on the Cape Henlopen sandflat. Relationships expressed as # style loss events/total # condition occurrences. Numbers in parentheses refer to events caused by low salinity (CURTIS AND HURD, 1980).

		Low	Tidal		Total
			High	Other	
S	Dawn	5/5	3/4	1/1	9/10
O	Dusk	3/3	1/4	None	4/7
L	Other	(1) + 2/7	1/6	(1) + 1/2	(2) + 4/15
A	Total	(1) + 10/15	5/14	(1) + 2/3	(2) + 17/32
R					

two high-marsh-ditch studies (Figures 1c and d), which were carried out simultaneously with the sandflat studies depicted in Figures 1a and b, respectively.

In order to analyze the relative effects of solar and tidal stages on style loss, we extracted from the seven Henlopen studies all style loss events, by our 3/10 or fewer criterion, along with the associated solar and tidal conditions. Temporally adjacent samples meeting our criterion were lumped as one event (*e.g.*, Figure 1f, 0600-0900). These data are summarized in Table 3, and show that style loss is most consistently related to dawn, regardless of tidal stage. Style loss occurred during 90% of all dawn periods sampled. When low tide occurred at dawn and dusk, style loss occurred 100% of the time, but style loss was not consistently associated with low tide at other times of the day. Style loss occurred during two periods of low salinity (15 and 10‰) on the sandflat, and these events are indicated in the table.

DISCUSSION

Ilyanassa obsoleta is a widespread and abundant species in estuaries along the eastern coast of North America (SCHELTEMA, 1964). The crystalline style of *I. obsoleta* is an important adaptation associated with nutrient procurement. Occurrence of a true crystalline style in a neogastropod is rare and perhaps unique. Therefore, investigation of the factors which influence its pattern of occurrence in these snails is pertinent to enhancing our understanding of the ecological niche of an important deposit-feeding species. Data presented here, in combination with data from previous studies (CURTIS, 1980; CURTIS & HURD,

1980; CURTIS & HURD, 1981), provide a basis for summarizing our current understanding of the factors involved with style occurrence.

Results of the present study quantitatively confirm the idea put forth by CURTIS (1980) that the style waxes and wanes on a daily basis, and that other than salinity (CURTIS & HURD, 1980) dawn is the only consistent environmental correlate to style loss. There appears to be synergism between low tide, and dawn and dusk, such that style loss is assured when these approximately co-occur. High tide appears to be irrelevant as a single factor, and low tide as a single factor only inconsistently correlates with style loss.

ROBERTSON (1979) suggested that *Ilyanassa obsoleta* styles are lost at low tide in manifestation of a feeding rhythm. This contention is not supported by results reported here.

In addition to solar and tidal influences on style occurrence, salinity is known to affect the style. CURTIS & HURD (1980) have shown through laboratory experiments that styles are lost when snails are exposed to salinities in the range of 20 - 15‰ or less. These results were confirmed by field observations during the style studies. Virtually all samples from these studies were collected when salinity was 20‰ or above. However, on five occasions (two on the sandflat in 1978; three in the marsh in 1979), salinity dropped into the 16-10‰ range, and on four of these occasions 3/10 or fewer snails had styles, indicating a significant negative effect on style occurrence. In retrospect, it is worth noting that the two occasions in 1978 co-occurred with dawn and low tide (see CURTIS, 1980, fig. 1b, both dawns where 0/10 snails had styles). These two events might, therefore, be explained by either dawn-low tide or low salinity.

Another factor thought to influence style occurrence is the presence of food in the gut. BROWN (1969) conveyed the idea that style presence is correlated with presence of vegetable material in the gut, whereas when meat is present, the style should be absent. ROBERTSON (1979) noted that for his snails styles were lacking when food was absent from the gut. Our studies (CURTIS, 1980; CURTIS & HURD, 1981) indicate that style presence is consistently dependent on neither the presence of material nor type of material in the gut, and that the style cycle represents a passive digestive rhythm rather than an active feeding rhythm. It remains to be seen whether food presence, absence or type can have any affect on the style cycle. At present there is no evidence to this effect.

Perhaps most important to a total perception of crystalline style behavior is the indication that pattern of style occurrence is not everywhere the same, even within the same general habitat. We have shown that at one salt marsh site (mouth-of-ditch) snails demonstrate a style cycle similar to that observed in the sandflat population, whereas snails at another site in the marsh (high-marsh-ditch) apparently do not exhibit such a cycle. Several sites along the shore near MLW have been used at Henlopen as sampling locations for style occurrence studies. The described pattern is apparently general there. In the salt marsh, however, it appears that some localized factor(s) can override the usual style cycle.

At this time, then, a number of factors that influence style occurrence in *Ilyanassa obsoleta* have been identified, including time of day, stage of tide, salinity, and perhaps feeding activity. Questions arising include:

- 1) Is the style cycle an endogenous rhythm?
- 2) What is the physiological basis for the style cycle, and what are the local environmental factors which influence it?
- 3) Is there latitudinal variation in the style cycle?
- 4) Does the style cycle vary with snail age, reproductive state, or parasitism?

ACKNOWLEDGMENTS

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Spatial Segregation of Four Species of Turban Snails

(Gastropoda : *Tegula*)

in Central California

BY

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(4 Text figures)

INTRODUCTION

FOUR SPECIES OF GRAZING TURBAN SNAILS of the genus *Tegula* are abundant in central California (ABBOTT & HADERLIE, 1980). Two of these species, *Tegula funebris* (A. Adams, 1855) and *Tegula brunnea* (Philippi, 1848), are common in rocky intertidal communities; *T. funebris* is abundant from mean lower low water (MLLW) to 1.5 m above MLLW, and *T. brunnea* is common below 0.5 m above MLLW. In addition, *Tegula pulligo* (Gmelin, 1791) and *Tegula montereyi* (Kiener, 1850) are common subtidally in kelp forests. LOWRY, McELROY & PEARSE (1974) studied the distribution of the 3 subtidal species at one location within the middle of a kelp forest off Pacific Grove, California; the snails were associated with specific algae on the bottom as well as throughout the water column on fronds of giant kelp plants (*Macrocystis pyrifera*). In the present paper, we describe the horizontal and vertical distribution of all 4 species of *Tegula*, from the intertidal zone to the seaward edge of a kelp forest, at the same location as the LOWRY, McELROY & PEARSE (1974) study. Distributions of the snails in early spring, when kelp biomass and canopy are minimal, are compared with their distributions in late summer, when kelp biomass and canopy development are maximal.

METHODS

Our study was conducted at Hopkins Marine Life Refuge in Monterey Bay off Pacific Grove, California. The habitat is very heterogeneous with a granite substrate interspersed

with sand channels, pinnacles, cracks, and boulders. The substrate is covered with a lush understory of *Cystoseira osmundacea*, many species of red algae, and a dense algal-invertebrate turf of coralline algae, tunicates, bryozoans, solitary corals, sponges, vermetids, and many other encrusting organisms. The dominant, canopy-forming plant is the giant kelp *Macrocystis pyrifera*. A detailed description of the study area is provided in PEARSE & LOWRY (1974).

Sampling was done using SCUBA in March 1977 and again in August 1977 along a 300 m transect that extended from the intertidal zone seaward through the kelp forest to a depth of about 13 m (Figure 1). Nine stations were established along the transect at about 1.5 m increments of increasing depth beginning at the intertidal level



Figure 1

Hopkins Marine Life Refuge, Pacific Grove, California, showing the nine sampling stations transecting the intertidal zone, shallow subtidal zone and kelp forest (hatched). Drawn from an aerial photograph taken on June 14, 1978

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of 1.5 m above MLLW. Populations of *Tegula* spp. were sampled at each station in two ways, depending on whether they occurred on giant kelp plants or on the "bottom" which included algal-invertebrate turf and understory plants as well as rock and sand. At each station, approximately 200 individuals of *Tegula* spp. were collected from the bottom. Giant kelp plants were present only at stations 3 to 9; at these stations, snails were collected from the nearest giant kelp plant that extended up the water column to the surface. All snails were removed from the selected kelp plants in 1.5 m increments of increasing depth from the surface to the bottom; snails from each sample level were placed in a separate plastic bag. The snails were identified, counted and measured to the nearest mm in the laboratory.

The data were analyzed for relative frequency and size distribution of each species on the bottom and on kelp plants at each station. The relative frequencies of each species on kelp plants at each station also were calculated for each 1.5 m depth interval in the water column. Our sampling design did not provide estimates of the densities of each species along the transect because determining densities requires additional labor-intensive estimates of the number of snails per unit bottom area, per kelp frond and the density of kelp fronds at each station.

RESULTS

In March each of the 4 species of *Tegula* showed a distinct zone of abundance on the bottom from the intertidal zone to the seaward edge of the kelp forest (Figure 2). *Tegula funebris* was restricted to the intertidal region from about 1.5 m above MLLW to 0.5 m below MLLW. *Tegula brunnea* occurred between 0.5 m to 7 m below MLLW. Near the shoreward edge of the kelp forest, at a depth of 3 m, nearly 90% of the turban snails on the bottom were comprised of *T. brunnea*. *Tegula montereyi* had a broad zone of distribution across the kelp forest, and except for a peak relative frequency of 50% at the 6 m depth, *T. montereyi* did not exhibit a clear dominance in relative frequency at any location. The relative abundance of *T. pulligo* on the bottom increased rapidly in the middle of the kelp forest at depths of 4 to 7 m. This species predominated in the seaward half of the kelp forest, with relative frequencies of 70% at a depth of 7 m to 100% at the 13 m depth.

The distribution of turban snails on giant kelp plants along the transect was similar to that of the snails on the bottom (Figure 2). *Tegula brunnea* was dominant on plants at the shoreward edge of the kelp forest. *T. pulligo*

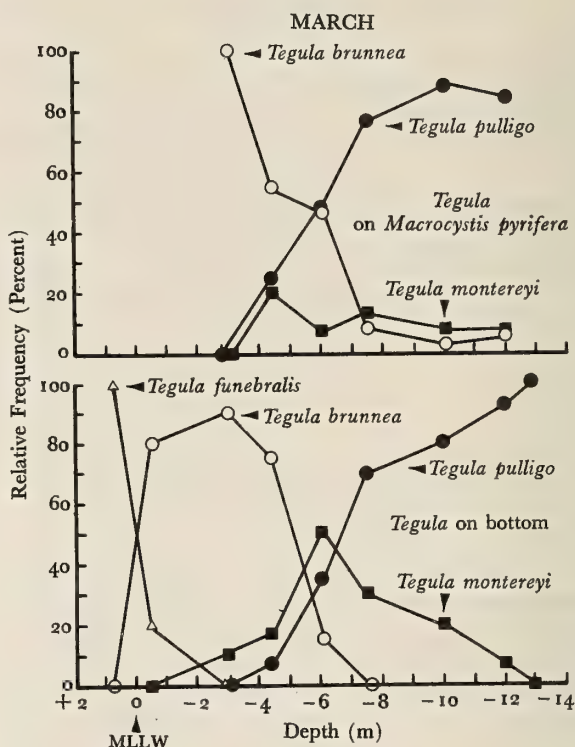


Figure 2

Distribution of four species of *Tegula* on the bottom and on giant kelp plants along the transect in March, 1977. The relative frequencies that each species comprised are plotted for each station. Snails on the bottom were sampled separately from snails on kelp plants. At each station, about 200 snails were collected from the bottom, and all snails were collected from single large kelp plants present at stations between depths from 3 to 12 m. Sample sizes for snails on kelp plants are shown in Figure 4

predominated on plants at the seaward portion, and *T. montereyi* occurred at low relative frequencies on plants throughout the middle of the kelp forest.

The pattern of zonation along the transect in August was remarkably similar to that in March for all 4 species, both on the bottom and on kelp plants (Figure 3). However, at 0.5 m depth *Tegula funebris* occurred with higher relative frequency in August than in March and *T. brunnea* occurred at correspondingly lower frequency. *T. brunnea* was present at higher relative frequencies in August than in March at the 4 to 6 m depths, both on the bottom and on kelp plants. *Tegula montereyi* did not

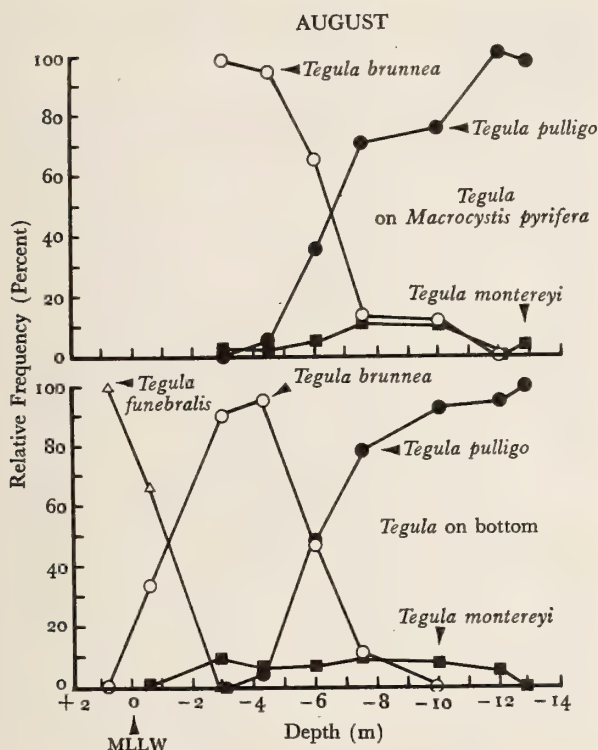


Figure 3

Distribution of four species of *Tegula* on the bottom and on giant kelp plants in August, 1977. Sampling procedures as explained in Figure 2

attain relative frequencies in the middle of the kelp forest as high in August as in March. The distribution and relative abundance of *Tegula pulligo* remained similar during both sampling periods.

The vertical distributions of turban snails on giant kelp plants did not show patterns of zonation that were as distinct as the horizontal distributions (Figure 4). *Tegula brunnea* in the shoreward part of the kelp forest showed a shift in relative abundance from the deeper portions of the plants in March up into the canopy in August. At the seaward stations, *T. brunnea* was generally evenly distributed throughout the water column at both sampling periods. *Tegula montereyi* occurred at about equal relative frequencies throughout the water column on kelp plants during both sampling periods. Similarly, *T. pulligo* was found at all depths on kelp plants with little apparent vertical zonation. However, in the middle of the kelp for-

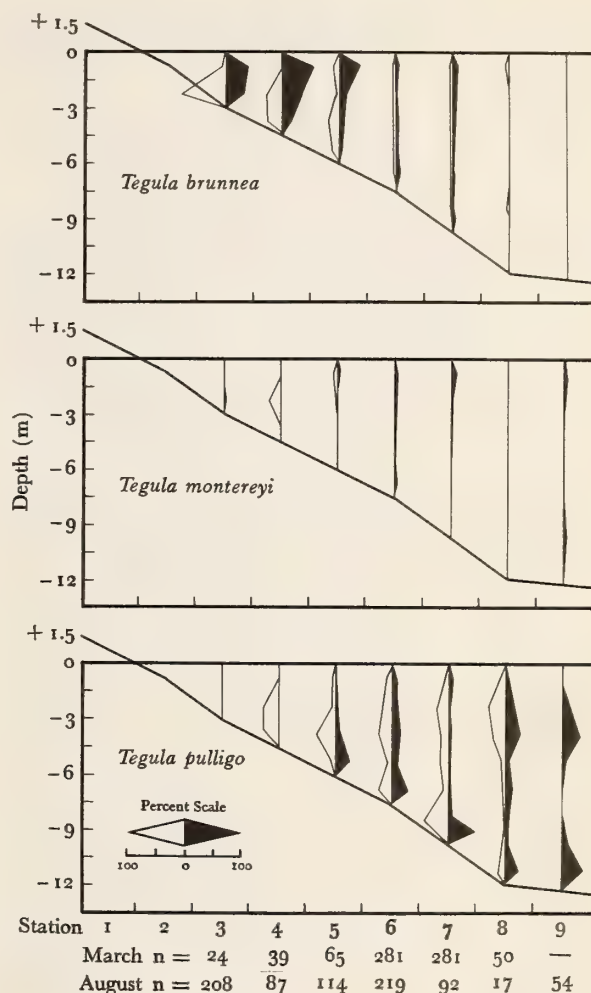


Figure 4

est, there were proportionately fewer individuals of *T. pulligo* near the top of the plants in August than in March. The size distribution of snails on the plants were similar to those found by LOWRY, McELROY & PEARSE (1974); individuals of *Tegula brunnea*, *T. montereyi* and *T. pul-*

ligo were smaller on the bottom, and in the lower portions of the kelp plants, than on the upper portion of the kelp plants.

DISCUSSION

Kelp forests are complex structural communities (PEARSE & GERARD, 1977) and closely related species often exhibit zonal patterns of distribution from the intertidal zone to increasing depths, *e.g.*, abalones (TUTSCHULTE, 1976); bryozoans (BERNSTEIN & JUNG, 1979); scorpaenid fish (HALLACHER, 1977; LARSON, 1980); and spider crabs (HINES, 1981). The 4 sympatric species of *Tegula* in the present study similarly exhibited a well-defined pattern of spatial segregation in the Hopkins Marine Life Refuge. *Tegula funebris* occurred exclusively in the intertidal zone. *Tegula brunnea* was dominant from the low intertidal zone through the shoreward portion of the kelp forest, while *Tegula pulligo* dominated the seaward portion of the kelp forest. *Tegula montereyi* usually occurred at low relative frequencies throughout the kelp forest, with the highest relative abundance near the middle of the forest. This pattern of zonation was consistent both on the bottom and on the giant kelp plants, and it changed little seasonally.

The vertical distribution of the three species of *Tegula* on fronds of *Macrocystis pyrifera* showed no clear pattern of zonation in either March or August. However, in the shoreward portion of the kelp forest individuals of *T. brunnea* were more frequent and individuals of *T. pulligo* were less frequent in the kelp canopy in August than in March. LOWRY, McELROY & PEARSE (1974) also found a vertical stratification with *T. brunnea* predominating in the canopy and *T. pulligo* predominating near the bottom. Their study was done near the center of the kelp forest (6-9 m depth) during August. Our more extensive sampling across the forest in March and August indicates that vertical stratification between these two species is very unstable.

Considering the marked seasonal changes in biomass and density of kelp plants in the Hopkins Marine Life Refuge (GERARD, 1976), the lack of substantial seasonal changes in the relative distribution of the different species of turban snails is surprising. Proliferation of kelp fronds in summer results in a tremendous increase in available substrate area at the sea surface, whereas winter storms greatly reduce the canopy cover. Moreover, winter storms probably knock many snails off the kelp fronds. The effect of the winter storm swells is most pronounced in shallower

water, and may account for the seasonal shifts of *Tegula brunnea* on the plants of the shoreward portion of the forest.

The mechanisms maintaining the zonation pattern of the 4 species of *Tegula* in the Hopkins Marine Life Refuge are not apparent. The upper distributional limits of many intertidal species may be determined by physical factors or behaviors that avoid adverse physical factors (*e.g.*, WOLCOTT, 1973). In this respect, *Tegula funebris* may be able to withstand temperature and desiccation stresses encountered in the intertidal area better than the other 3 species, thereby partially accounting for the near complete dominance of *T. funebris* in the intertidal zone. However, such a physiological mechanism would not account for the observed lack of *T. funebris* subtidally, or the zonation of the subtidal species.

Gradients of water turbulence and light could be important in determining the zonation patterns of the subtidal species. If, for example, individuals of *Tegula brunnea* were better able to maintain a grip on substrates in strong surge than those of *T. pulligo*, they might be expected to predominate in high-energy areas of the shallow subtidal zone and inner edge of the kelp forest. The zonation pattern of the snails also might be the result of pronounced dietary preferences for particular algal species limited to particular depths by specific light requirements. However, LOWRY, McELROY & PEARSE (1974) found that all 3 subtidal species were widely distributed on different species of algae in the middle of the kelp forest, and all were found most frequently on giant kelp plants. Moreover, all 4 species have a high preference for *Macrocystis pyrifera* for food (unpublished observations; James M. Watanabe, pers. comm.). Considering the enormous abundance of giant kelp, both as attached plants and as pieces of plants on the forest floor (GERARD, 1976), competition among these snails for a limited food resource is unlikely, and differences in food preferences and availability probably cannot account for the subtidal zonation pattern. Furthermore, we have not observed any behavior in the field or laboratory that could be categorized as interference competition (*sensu* COLWELL & FUENTES, 1975) among any of these species.

Predation often limits the lower distribution of intertidal organisms, and in some areas predation by sea stars and whelks may determine the lower limit of *Tegula funebris* (PAINE, 1969; B. MENGE, 1972; J. MENGE, 1974). Predation by rock crabs, *Cancer antennarius*, also could be important. These crabs cannot crack the shells of *Tegula brunnea* as easily as those of *T. funebris* (ABBOTT & HADERLIE, 1980), and their presence in the low

intertidal area might provide an explanation for the replacement of *T. funebris* by *T. brunnea* in the shallow subtidal zone. However, individuals of *C. antennarius* are very scarce in the Hopkins Marine Life Refuge (Hines, in press), and the small number of crabs there is unlikely to have much impact on the large snail populations.

Sea stars are important predators in the subtidal kelp forest of the Hopkins Marine Life Refuge, and *Tegula* spp. are highly preferred prey of *Pisaster giganteus* in particular (HARROLD, 1981). WATANABE (1980) found that high water movement and dense cover of red algae in the shallow subtidal area provided turban snails with some refuge from sea star predation. Snails within the kelp forest also may escape sea star predation by crawling up fronds of giant kelp plants (HARROLD, 1981). However, sea otters, *Enhydra lutris*, in the Hopkins Marine Life Refuge eat large numbers of turban snails collected from the kelp fronds (COSTA, 1978). The distributions and foraging patterns of all these different predators are not understood well enough to explain whether and how they might influence the distribution patterns of the subtidal species of *Tegula* in the Hopkins Marine Life Refuge.

Recruitment patterns may reflect and partly determine the distributions of the adult snails. Recruitment of *Tegula funebris*, for example, is restricted to the intertidal zone (PAINE, 1969). Moreover, Watanabe (pers. comm.) found distributional patterns of juvenile turban snails in the Hopkins Marine Life Refuge that were strikingly similar to those of the adults. Small juveniles (<5 mm diameter) of *T. brunnea* were most abundant on solid rock surfaces at depths less than 3 m, those of *T. pulligo* were mainly on shell fragments in the seaward portion of the kelp forest, and those of *T. montereyi*, were on shell fragments distributed throughout the forest. However, turban snails probably live at least for several years (FRANK, 1975), and they are very mobile. More knowledge of the movements and life history of these snails clearly is needed before the mechanisms that maintain their distinct patterns of distribution will be revealed.

SUMMARY

1. Three species of turban snails display distinct patterns of zonation between the intertidal area and the seaward edge of the giant kelp forest in the Hopkins Marine Life Refuge, central California. *Tegula funebris* is exclusively intertidal, *Tegula brunnea* is mainly shallow subtidal (0.5 to 7 m depth) in the shoreward portion of the kelp forest, and *Tegula pulligo* is mainly deeper (7 to 13 m depth) in the seaward portion of the kelp forest.

2. A fourth species, *Tegula montereyi*, occurs subtidally throughout the kelp forest, but does not dominate any particular zone.
3. The 3 subtidal species of *Tegula* are distributed: snails in the Hopkins Marine Life Refuge were very throughout the water column on giant kelp plants, *Macrocystis pyrifera*, from the surface canopy to the bottom holdfasts, in the same pattern as their bottom distributions. *Tegula brunnea* is mainly on plants in the shoreward portion of the forest, *T. pulligo* is mainly on plants in the seaward portion of the forest, and *T. montereyi* is distributed more or less evenly on the plants. There is little distinct pattern of vertical distribution on the plants of any of the species of *Tegula*.
4. The patterns of distribution of the 4 species of turban similar in March and August, 1977, except that in August *Tegula brunnea* was most frequent in the canopy and *T. pulligo* was most frequent near the bottom of the plants.
5. Although recruitment patterns of juveniles reflect adult distributional patterns, the mechanisms maintaining these distributional patterns remain unclear. Tolerance to aerial exposure may permit *Tegula funebris* to thrive in the intertidal zone, and lack of such tolerance may exclude the other species from this zone. Effective defense from predation and tolerance to high water turbulence may permit *T. brunnea* to dominate in the shallow subtidal, while *T. montereyi* and *T. pulligo* may escape predation in deeper waters by crawling up kelp fronds.

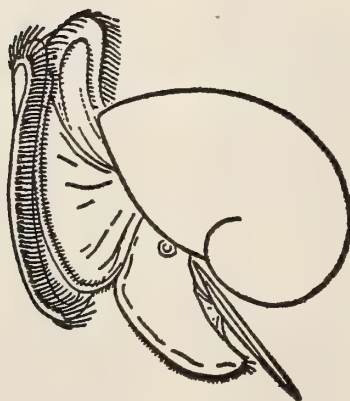
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Diet and Reproductive Biology of the Rocky Intertidal Prosobranch Gastropod *Tricolia pulloides*

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(5 Text figures)

INTRODUCTION

ALTHOUGH *Tricolia pulloides* (Carpenter, 1865) is a common inhabitant of the intertidal region on California rocky shores, it is small and often overlooked. Very little is known of its natural history. A related European species, *Tricolia pullus* (Linnaeus, 1758), has been studied extensively; *T. pullus* feeds on diatoms (FRETTER & GRAHAM, 1962). Females shed their eggs singly into the water. Development is pelagic, and the embryos, unlike those of many prosobranchs, pass through a free-swimming trochophore stage (LEBOUR, 1937; FRETTER, 1955). A related Indo-Pacific form, *Tricolia* (formerly *Hilola*) *variabilis* (Pease, 1861) has been studied in Hawaiian inshore waters where it is abundant. The species is sexually dimorphic. The eggs, often laid on the brown alga *Padina*, exhibit direct development and hatch as juvenile snails, thus omitting a pelagic larval phase (WERTZBERGER, 1968a, b; KAY, 1979).

Studies of *Tricolia pulloides* were conducted on the population in the midtide zone dominated by the red algae *Rhodoglossum affine* (Harv.) Kyl. and *Gigartina papillata* (C. Ag.) J. Ag. at Mussel Point, Pacific Grove, California, in the period April 1979 to June 1980. One objective was to examine the food and feeding habits of the snails, answering the questions: What are they eating? Where are they obtaining food? When are they eating? The second objective was to characterize reproduction and development in the species through studies of the annual cycle of reproduction and growth, the nature of the egg masses deposited by females, and the gross sequence and timing of events in embryonic development.

FOOD STUDIES

Materials & Methods: To determine what *Tricolia pulloides* was eating and where the food was obtained, 5 snails were collected from each of 5 species of red algae: *Gigartina papillata*, *Gigartina leptorhynchus* J. Ag., *Gastroclonium coulteri* (Harv.) Kyl., *Rhodoglossum affine*, and *Cryptosiphonia woodii* (J. Ag.) J. Ag. All collections were made at or below the 1.5 ft. (45 cm) tidal level. The larger, more conspicuous snails were collected, without scrutinizing the algae for juvenile individuals. Each sample was placed directly in 5% formalin. The stomach of each snail was dissected out, and the contents placed on a slide in a drop of 30% corn syrup under a coverslip for viewing under a compound microscope. Stomach contents were identified with the assistance of Dr. Isabella Abbott. The large pennate diatoms present in the preparations were counted; the relative abundance of other materials was estimated.

To determine when *Tricolia pulloides* was eating over the tidal cycle, hourly samples, each of 5 snails, were collected from a horizontal rock face covered with *Rhodoglossum affine* about 0.5 ft. (15 cm) above zero tide level. Samples were taken over a 7 hour period. The samples were preserved, and gut contents analyzed as before.

Results: Between 90 and 95% of the contents of stomachs of snails from all 5 types of algae consisted of pennate diatoms. Five to ten percent of the gut contents consisted of small sponge spicules, unidentifiable organic matter termed detritus, and small pieces of epiphytic algae including coccoid blue-greens, *Dermocarpa* sp., *Collinsella tuberculata* S. & G., and Florideophycids. No one of these categories normally comprised more than 1-2% of the total diet. The diatoms and other algae in the gut were browsed as epiphytes on the surfaces of macroalgae. *Tri-*

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colia pulloides was never found feeding on encrusting algae, rocks, or exposed surfaces.

epiphytic algae also occur in the areas browsed for diatoms and may be rasped up unintentionally. No single component comprises a large portion of the incidentals.

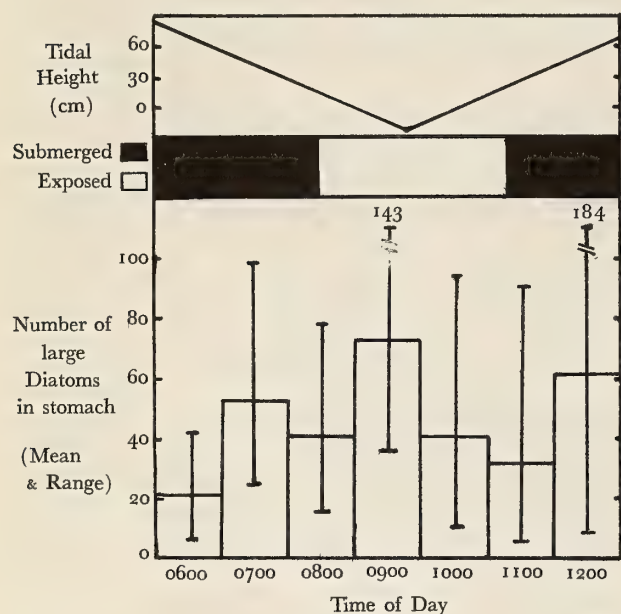


Figure 1

Number of large Diatoms in the stomachs of *Tricolia pulloides* at different phases of the tidal cycle

Figure 1 shows the results of sampling the gut contents of the *Tricolia* population over a 7 hour period centering on low tide. Quantity of food in the gut is shown in terms of number of large diatoms counted in squashes of the stomachs of the 5 snails sampled each hour. The population showed great variability, and the differences between sample means are not significant, but diatoms were most abundant in the stomachs at low tide.

Discussion: The diet studies show that *Tricolia pulloides* skims the surface of macroalgae, taking very largely pennate diatoms. CHUN (1979) has noted large populations of sessile pennate diatoms on ungrazed, distal areas of fronds of *Rhodoglossum affine*, and noted a significant reduction in these populations through grazing by *T. pulloides* and other small herbivorous gastropods. Further, when submerged at high tide, *T. pulloides* tends to move out to these distal areas of algal fronds (FOSTER, 1979). The 5-10% of the diet not consisting of diatoms can probably be considered incidental. Particulate matter and

REPRODUCTIVE BIOLOGY

Materials & Methods: The following data were recorded for all snails collected: shell length from tip of spire to base of aperture, sex, and (for females) the number of mature eggs within the ovary. Sex was determined by cracking the shell in a small turnbuckle, removing the shell, and examining the gonads under a dissecting microscope. In females the gonad is translucent and bears large yellow eggs of uniform size. In males, the gonads are mottled and white.

To determine the annual reproductive cycle of *Tricolia pulloides*, monthly samples of *Gigartina papillata* and *Rhodoglossum affine* were taken from the same rocky area at the 0-1.5 ft. (0-45 cm) tide level at Mussel Point and were examined carefully for gastropods. All *T. pulloides* on fronds and holdfasts were removed and preserved in 5% formalin prior to dissection. The algal fronds were also checked for egg clutches of *T. pulloides*.

The egg masses of *Tricolia pulloides* were first identified as such by noting the great similarity between the large eggs in the ovaries of ripe females and the large eggs in certain egg masses commonly found on plants inhabited by *T. pulloides*. Laboratory observations of egg-laying and hatching confirmed the identification.

Yellow egg clutches were collected in the field from areas of dense *Tricolia pulloides* populations. Record was kept of the location of the egg masses on the algal frond, the type of alga bearing the egg mass, the diameter of the egg mass, and the number of eggs contained within the egg mass. The algal fronds bearing masses were then maintained in 12.5 cm diameter fingerbowls of seawater at about 14°C. The water was changed twice daily, and the samples were checked daily under a dissecting microscope for stage of development.

To see if *Tricolia pulloides* would lay egg clutches consistently under laboratory conditions, 2 fingerbowls of 25 snails each were kept with 6-8 clumps of *Rhodoglossum affine* free of any previous egg clutches and other organisms, at about 14°C. Daily the water was changed and the *R. affine* fronds were checked. All new egg masses found were measured and the eggs were counted. Each clutch was then trimmed from the algal frond, placed in a depression slide with a coverslip, examined under a compound microscope, and the time and stage of development noted. These egg masses were then put in fresh

seawater in fingerbowls, kept at 14°C, and the seawater changed twice daily. Five selected clutches were checked microscopically twice daily for general developmental features, and three other clutches were checked every half hour each day up to the time of hatching, to establish the time scale of development under these laboratory conditions.

Hatchlings from these clutches were kept on fronds of *Rhodoglossum affine* under the same laboratory conditions as those used for the observation of clutches. The diet of the hatchlings was determined by lightly squashing the bodies of five-day-old snails in 1 drop of 30% corn syrup between a slide and coverslip and viewing them under a compound microscope.

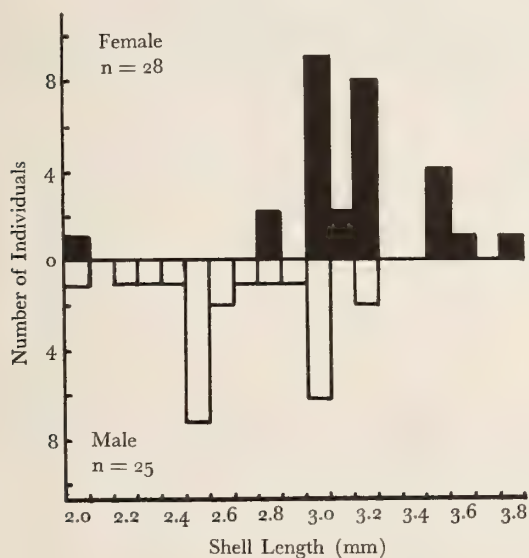


Figure 2

Size-class distribution of females and males of *Tricolia pulloides* in May 1979

Results: Figure 2 shows a distribution by size and sex of the 53 individuals 2.0 mm or more in shell length that were taken for diet studies (juvenile animals less than 2.0 mm long were not adequately represented in the sample). In this May 1979 sampling, males and females occurred in approximately equal numbers. Female snails averaged significantly larger than the males ($p < 0.001$); the mean shell length for females was 3.14 mm ($n = 28$), and for males was 2.62 mm ($n = 25$).

In the yearly cycle of the population (Figure 5), ripe females appear first in March. Examination of algal

fronds shows that egg clutches are deposited only in May, June, and July. Thereafter the larger snails disappear from the population, leaving the small snails as a new year-class.

The eggs appear to mature rapidly and simultaneously in the ovary, for all individuals found either lacked enlarged ova or had full-sized eggs. The number of enlarged eggs counted in the ovary of individual females ranged from none (in one case) to 206, with a mean of 56.5 for 30 females (Figure 3). The number of eggs in an ovary tends to increase with the size of the female, but the variability at any particular shell length is great.

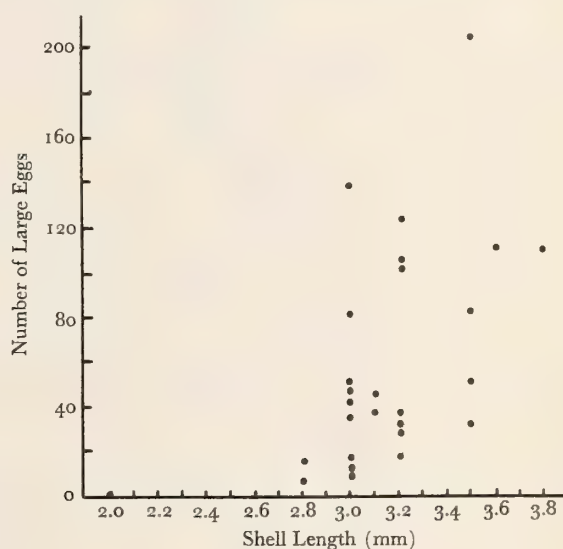


Figure 3

Relation between size (shell length) and number of large eggs in the ovary of female *Tricolia pulloides*

Fifty snails kept in fingerbowls in the laboratory at 14°C laid 57 egg clutches over a 6 day period. The number of eggs per clutch ranged from 11 to 104 with a mean of 32.5. These eggs in newly laid clutches appeared identical to those in the ovaries of mature female *Tricolia pulloides*. These eggs are light yellow, opaque, show a gradient in distribution of yolk, and each is enclosed in a colorless transparent capsule. The eggs and egg capsules are approximately 150 μ m and 180 μ m in diameter, respectively. Generally, the eggs are laid in a compact, sinuous ribbon which is coated with a clear jelly. The completed egg clutches are disc-shaped, average about 2.0 x 2.5 mm in diameter, and are attached by one flat surface to a plant. They are most generally found on a concave surface at the

bifurcation of a frond on such red algal species as *Rhodoglossum affine*, *Gigartina papillata*, and *Gigartina leptorhynchos*, but some are found on *Cryptosiphonia woodii* which does not have a concave surface.

The time schedule of development, based on the external morphology of the embryo or larva, is shown in Figure 4. Zero time is the time the egg clutch was deposited; the time of fertilization is unknown. The first 6 cleavage stages

each lasted from 0.5 to 1 hour. A few eggs showed abortive development; they became white and took on a granulated appearance after a few hours. By 24 hours the larval shell appeared complete. At about this time the tissues at the posterior end of the shell began to turn light green. The soft body parts pulled away from the interior of the shell antero-dorsally by 1.8 days, and soon portions are seen extending from the aperture. Pedal cilia and the oper-

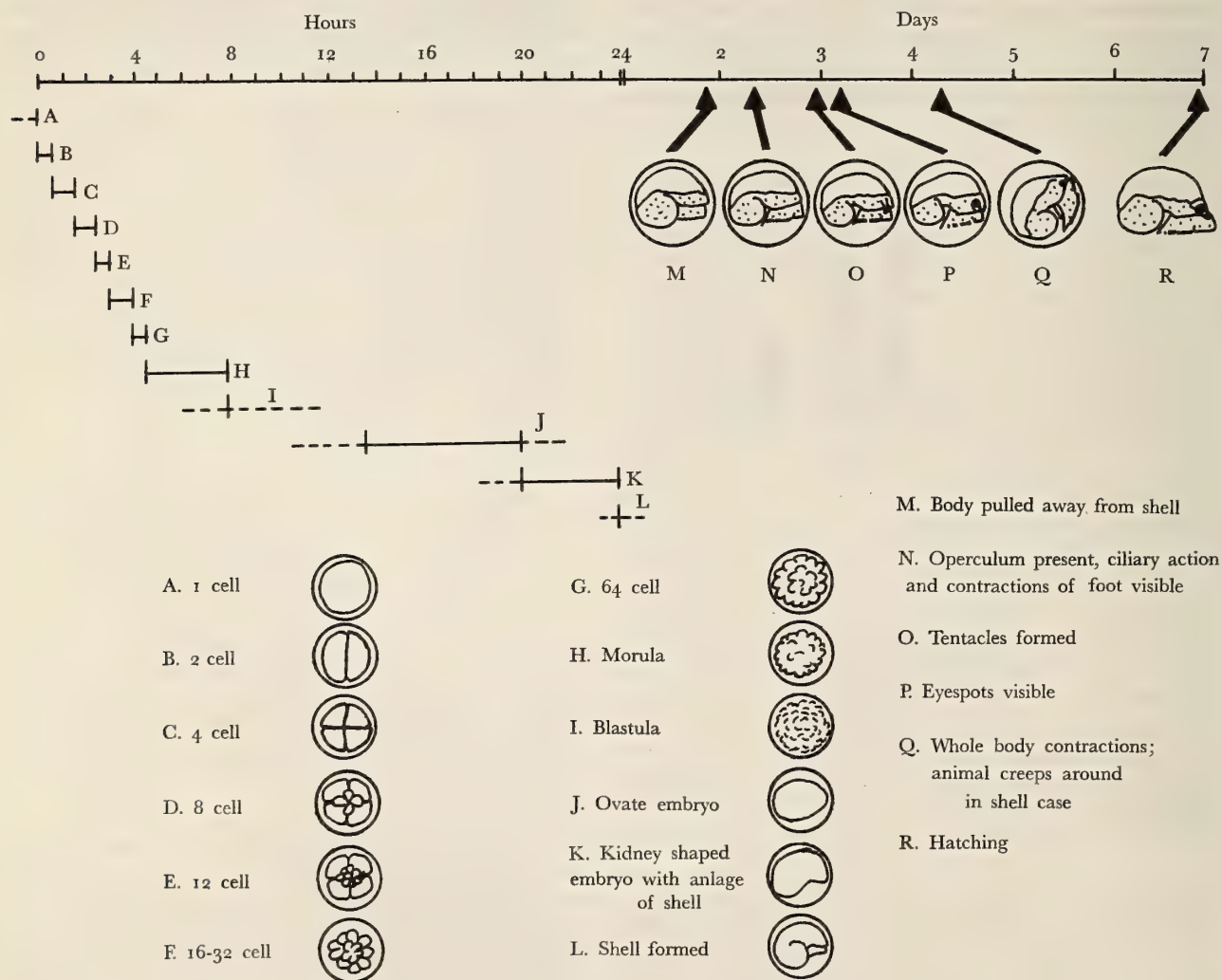


Figure 4

Average rate of development of *Tricolia pulloides* at 14°C. Solid bars show beginning and end of a stage. Bars ending in dotted lines indicate the approximate times certain features occurred whose exact beginnings and ends could not be determined accurately.

culum were formed by 2.3 days. Within 2 hours muscular contraction of the foot was seen. By 3.1 days the tentacles were present, and shortly thereafter black eyespots appeared. Contraction of the body into the shell and closure of the operculum were seen at 4.3 days. Soon the embryos began occasional rotations, crawling on the interior of the transparent egg capsule. Frequency of rotation increased just prior to hatching, and the jelly coating began to dissolve away about this time. At 7 days the embryos hatched as miniature young snails with nearly clear, planospiral shells, and with light green pigment concentrated in the area of the visceral hump. The maximum diameter of the shell at hatching was $240\text{ }\mu\text{m}$.

After hatching, the hatchlings move out on the algal frond where they cling tenaciously from the very start. They are not swept away by a jet of water forcefully extruded from an eyedropper pipette. Snails knocked over maintain position by a mucus thread extruded by the foot. Whole mounts of 5-day-old snails crushed under a coverslip show that the young are eating primarily small, naviculoid diatoms. By 5 days after hatching, the shell aperture has widened with new shell growth. The body tissues are still relatively clear, except for the posterior parts of the visceral hump which are yellow and darker green. New shell is more darkly tinted and translucent. These juvenile snails were commonly found in the sandy holdfasts of algae in the midtide zone.

Discussion: Egg-laying in *Tricolia pulloides* occurs from May through July. From August 1979 to February 1980 snails bearing eggs were not seen (Figure 5). Snails less than 0.5 mm in length are very difficult to sex because of their small size, but even among larger snails, animals with eggs were unexpectedly scarce in the population sampled in 1980. This might be due to a sex ratio deviating from 1:1 or to a differential distribution of males and females in the habitat until late in the reproductive cycle, or possibly to protandric hermaphroditism. Finally, perhaps the sexes are indistinguishable by macroscopic features until near sexual maturity at 9-11 months of age, when eggs rapidly enlarge in the ovaries of large females. I am unable to evaluate these possibilities.

Since the ovary in most of the females examined contained more eggs than occurred in the average clutch (32), and great variability exists in the number of large eggs in females of a particular length, it seems likely that a female does not put all her eggs in one basket, so to speak, but instead lays two or more clutches for a given group of mature oocytes.

Tricolia pulloides has many features suiting it for laboratory studies. Egg clutches are easily obtained in the

laboratory. No special conditions were required to stimulate egg-laying. The egg is large and yolky, and early

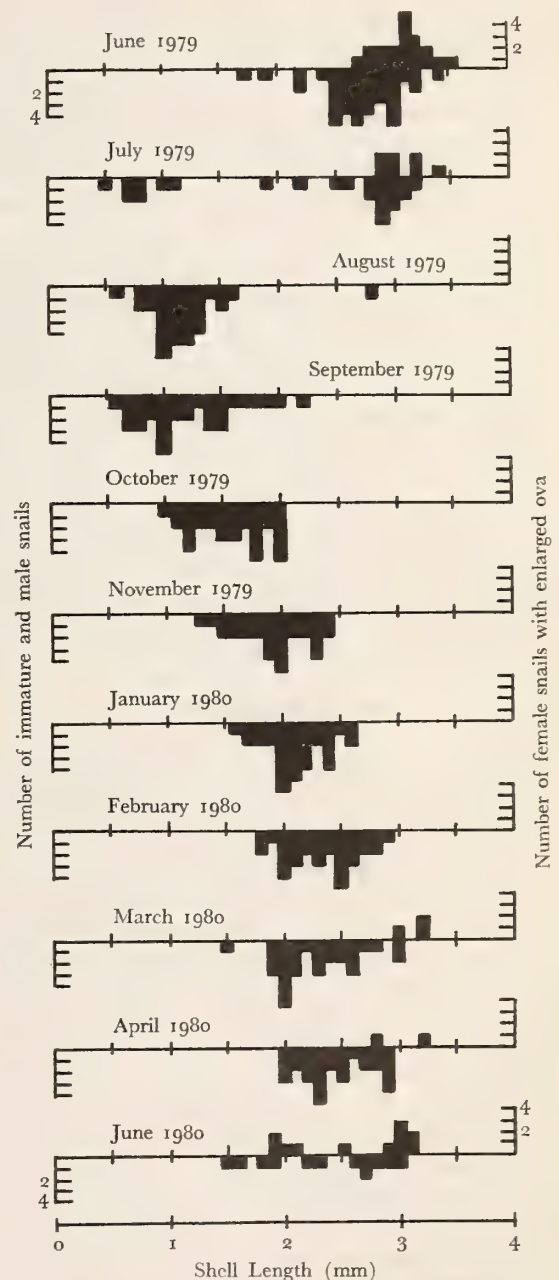


Figure 5

Size-class distribution of the *Tricolia pulloides* population (immature and male snails below horizontal line, ripe females above) in approximately monthly samples from Mussel Point, June 1979 to June 1980

development is quick and easy to follow. Development from egg-laying (fertilization?) to hatching takes only about 7 days at 14°C, and at this temperature most eggs developed normally. However, at room temperature (about 23°C) many eggs failed to develop or developed abnormally. Under intense light and moderate heat, embryos were seen to rotate much more frequently within the egg membrane. At low tide on warm days the egg clutches may sometimes be exposed to increased temperature, possibly affecting mortality and rate of development.

Tricolia pulloides has a relatively direct development and lacks swimming trochophore and veliger stages. In contrast, the British *T. pullus* develops via a free-swimming trochophore larva (LEBOUR, 1937). Direct development, bypassing a pelagic stage, is comparatively uncommon among prosobranchs (WEBBER, 1977), yet it has been documented in the closely related *Tricolia (Hilola) variabilis* (Pease, 1860) (see WERTZBERGER, 1968 a,b; KAY, 1979). The occurrence of direct development may help account for the somewhat patchy distribution of *T. pulloides* in the intertidal region. Where dispersal is probably mostly by creeping, local populations may develop. Further investigation of this would be desirable.

SUMMARY

1. The diet and reproductive biology of *Tricolia pulloides* was investigated during the period April, 1979 - June, 1980, at Mussel Point, Pacific Grove, California.
2. *Tricolia pulloides* feeds primarily on pennate diatoms grazed as epiphytes from fronds of such red algae as *Rhodoglossum affine* and *Gigartina papillata*. Small particles of detritus and pieces of other epiphytes are probably picked incidentally. Food is found in the gut at both high and low tide.
3. *Tricolia pulloides* shows roughly a 1:1 ratio of males and females during the most active reproductive period. Ripe females (averaging 3.14 mm in length) are very significantly larger than the ripe males (averaging 2.62 mm in length) though the smallest females are considerably smaller than the largest males.
4. *Tricolia pulloides* appears to have a life span of about a year. Sexual maturity and reproduction occur at 9 - 11 months.
5. The ovary in ripe females carried up to 206 and averages 56.5 yellow, yolky oocytes about 150 µm in diameter. Eggs are laid in a sinuous ribbon coated with clear jelly, the whole forming a disc-shaped clutch measuring about 2.0 x 2.5 mm, containing up to 104

eggs but averaging 32.5 eggs. Egg clutches are attached to red algal fronds in the midtide zone.

6. Eggs cleave spirally and development is direct. Within 7 days at 14°C they hatch as miniature snails that feed on naviculoid diatoms and cling tenaciously to algal fronds with the aid of mucus threads.
7. All stages of the life history are easily maintained in the laboratory, suggesting this might make a useful experimental animal.

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Growth Rates of *Penitella penita* (Conrad, 1837),
Chaceia ovoidea (Gould, 1851)
(Bivalvia : Pholadidae)
and Other Rock Boring Bivalves in Monterey Bay

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(3 Plates)

INTRODUCTION

MANY INVESTIGATORS over the years have attempted to elucidate the mechanisms utilized by marine bivalves in penetrating hard substrate such as rock. Up to 1968, however, very few studies had been made on actual growth rates of these rock borers. MACGINITIE & MACGINITIE (1949) reported that the common pholad *Penitella penita* (Conrad, 1837) could excavate a burrow 2.5 cm in diameter and 15 cm deep in 5 to 6 years, yet no details were given as to how these figures were determined. In 1968, EVANS (1968a, b, c, d) published a number of ecological studies on populations of *Penitella penita* which occur in the intertidal zone along the Oregon coast in and near Coos Bay. Included in these studies were the first careful investigations of growth rates of rock boring pholads.

TURNER (1954, 1955) pointed out the inverse relationship between substrate hardness and growth rates in rock boring pholads, so EVANS (1968d) chose study sites that had rock of different hardness in order that direct comparisons could be made. Geologists use the Mohs' hardness scale, with a range of 1 to 10, for arbitrarily assigning a measure of relative hardness to common minerals from soft talc to hard diamond. Yet no standard method for measuring the relative hardness of sedimentary rocks has been developed. EVANS (1968a) therefore devised a method for comparing the sedimentary rock hardness at his 3 study sites. Using a carborundum masonry drill bit, he determined the depth of holes drilled under constant time and force in different rock samples. In his study the sandstone at Fossil Point was softest, that at South Jetty

was twice as hard, and that at Cape Blanco was four times as hard.

In his growth rate studies, EVANS (1968d) used two methods, each employing native rock at various levels in the intertidal zone. First, he stripped off patches of pholad-infested rock exposing fresh unbored layers, then periodically for 36 months collected and measured the *Penitella penita* that had settled and burrowed into the substrate. Second, he extracted young *P. penita* from their natural burrows and introduced them into artificial burrows he had drilled with a star drill into rock of varying hardness. In the softest rock at Fossil Point he found that young *P. penita* bore to a final depth of 150 mm in 3 years, at which time the animals had a shell length of 55 mm and a diameter of 25.5 mm and were ready to metamorphose and form a callum. This boring rate of 50 mm per year was much faster than at the other two sites with harder substrate. At the South Jetty site he estimated the boring rates to be 2 to 50 mm per 3 years, and at Cape Blanco 4 to 50 mm per 12 years.

In Monterey Bay, sedimentary rock is found in the intertidal zone only in the area near Santa Cruz. The eastern and south-eastern parts of the Bay have sandy beach shorelines, and the south-western part of the Bay has a granitic shore that is impervious to borers. Several species of pholad and mytilid borers occur in the intertidal shale at Santa Cruz, and in the shale of the Monterey Formation in shallow subtidal waters throughout the Bay (HADERLIE, 1980a, c). For the past 6 years several species of these bivalve borers have been studied, and in a few cases growth rates over extended periods of time have been monitored.

METHODS

When this study was initiated it was the intent to use the same techniques employed by Evans so that comparisons could be made between the growth rates of California and Oregon populations of pholad borers. The study site in the intertidal zone at Santa Cruz was located on an exposed reef consisting of shale of the Monterey Formation with the substrate of varying types from relatively soft mudstone to hard chert (HADERLIE, 1980c). This reef had a bivalve borer population dominated by *Penitella penita* with lesser numbers of the pholads *Penitella gabbii* (Tryon, 1863), *Parapholas californica* (Conrad, 1837), *Chaceia ovoidea* (Gould, 1851), and *Netastoma rostrata* (Valenciennes, 1846), and the mytilids *Adula californiensis* (Philippi, 1847), *A. falcata* (Gould, 1851), and *Lithophaga plumula* (Hanley, 1843).

At Santa Cruz, the growth rate study concentrated on *Penitella penita*, but it proved impossible to use successfully those techniques employed by Evans on the Oregon coast. The layers of rock in the reef at Santa Cruz were too deformed to allow extensive stripping of the eroded superficial layers to expose unbored substrate, and the mortality rate of borers introduced into artificial burrows was extremely high. In addition, winter storm waves broke off massive areas of shale containing the experimental animals. It was therefore necessary to use different methods for determining growth rates.

In southern California, X-ray radiography has been used to study the geometric and spatial relationships of borings in sedimentary rock penetrated by bivalve borers (WARME & MARSHALL, 1969; WARME, SCANLAND & MARSHALL, 1971). Radiographic techniques have also been used successfully to monitor the growth rates of the wood boring teredinid *Bankia setacea* (Tryon, 1863) in Monterey Bay (HADERLIE & MELLOR, 1973). To my knowledge, however, no investigation of growth rates of stone borers using X-ray techniques has been carried out until the study being reported on here.

In order to monitor growth rates over an extended period of time using radiography it was necessary to have the living bivalve borers in portable, relatively flat pieces of shale that could be taken to the laboratory for X-ray analysis, then returned to the sea to allow for additional periods of growth. Small actively boring pholads and mytilids from the intertidal reef at Santa Cruz were removed from their burrows and introduced into artificial burrows drilled into the edges of flat shale slabs varying in thickness from 4 to 15 cm. The holes were drilled with a car-

borundum-tipped bit and varied in diameter so that each animal fitted snugly in the cylindrical burrow. After the bivalve was placed in the burrow, the open end was plugged with a perforated cork which allowed the siphons to protrude but prevented the animal from falling out of the burrow. The perforation in the closing cork varied from 10-12 mm in diameter and was made as large as possibly intentionally, for EVANS (1968b) found that smaller diameter openings retarded bivalve growth rates by possibly reducing food gathering ability.

At the beginning of this study, shale slabs of varying hardness quarried from the reef at Santa Cruz and from subtidal shale dredged off Monterey were employed as experimental substrate. To make comparisons easier, however, we early settled on shale of a hardness intermediate between the soft mudstone and the hard chert. The selected shale was of Miocene age and composed of clay and siliceous material derived from diatoms. The CaCO_3 content was very low, varying from 0.03 to 0.74%.

To have some comparative measure of hardness, the same technique EVANS (1968a) used in Oregon was employed. A series of holes (20 or more) were drilled under conditions of constant time and force, and hardness was determined by measuring the average depths of the resulting holes in the shale. A 6 mm diameter carborundum-tipped masonry bit mounted in a standard drill press rotating at 580 rpm was used. The drill press was modified so that the drill bit was applied to the shale surface with a constant weight of 6.8 kg (= 15 lbs), and the drill press was activated for exactly 2 seconds by a photographic timer.

In the moderately hard shale finally selected for use in these studies, the average depth of the test drill holes was 11.8 mm. EVANS (1968a) found 12.1 mm to be the average in stone from his Fossil Point site, so the stone used in this study is of about the same hardness as the softest stone Evans investigated in Oregon.

After the experimental animals were introduced into the artificial burrows in the shale, the shale slabs were placed in 50 x 30 x 30 cm polyethylene containers such as are used for holding cartons of milk, and the containers lowered to various depths in the water under Municipal Wharf No. 2 in Monterey. The water at the study site is essentially of the same quality as open Bay water (HADERLIE & DONAT, 1978). Some shale blocks were suspended in the intertidal zone, others were lowered to near the bottom. The depth of exposure was determined by where the experimental animals had been collected. For example, *Penitella penita* and *Lithophaga plumula* from the midintertidal level at Santa Cruz were suspended at the midintertidal level;

Chaceia ovoidea and *Penitella gabbii* from subtidal shale off Monterey were suspended near the bottom in 7 m of water.

At bimonthly intervals the shale slabs were recovered and taken to the laboratory for X-ray analysis. Except while being X-rayed the stone panels were maintained in aerated sea water. A Norelco Searchray, Type 1206, X-ray machine was used to expose the shale panels on Kodak NS-2T (no-screen medical) X-ray film. The exposure time was from 5 to 25 seconds, depending on shale thickness, with a power of 70 Kv at 2 milliamperes. Some panels with experimental borers served as controls and were treated exactly like the others, including trips to the laboratory, but were not X-rayed.

RESULTS

Since April 1978 when this investigation using radiography began, 191 individual pholads and mytilids have been introduced into artificial burrows for growth studies. Species represented were *Penitella penita*, *P. gabbii*, *Parapholas californica*, *Chaceia ovoidea*, *Netastoma rostrata*, *Adula californiensis*, *A. falcata*, and *Lithophaga plumula*. All of the pholads used were immature individuals still in the boring stage, and the mytilids were relatively small and therefore assumed to be young individuals.

Except for *Penitella penita* and *Chaceia ovoidea*, the mortality rate for the transplanted pholads was very high, even in the controls that were not X-rayed. Typically the animals would survive for 2 to 4 months without showing much growth or tunnel excavation, then would either be missing from the burrows, or only dead shell valves remained. In most cases the causes of the mortality were not known. Removing stone borers from their natural burrows without injuring them is difficult, and although care was exercised, it is possible that many did not survive due to injuries that were not apparent to the investigator. In some cases loss of experimental animals was clearly due to predation by the sea star *Pisaster brevispinus* (Stimpson, 1857) and possibly other asteroids (HADERLIE, 1980b). Attempts to exclude asteroids from gaining access to the experimental stone borers were only partially successful. The flatworms *Stylochus atentaculatus* Hyman, 1953, *S. californicus* Hyman, 1953, and *S. tripartitus* Hyman, 1953, were often found in the burrows where the bivalves were dead with only the shell valves remaining. EVANS (1967) reported that *Stylochus* sp. in Oregon was a predator on *Penitella penita*, being able to squeeze through a very narrow entrance hole to consume the soft parts of the bivalve.

The experimental mytilids in general had a higher survival rate than the pholads, but showed very little if any growth or burrowing activity. Figure 1 is an X-ray photograph of an experimental shale panel 3 cm thick and 28 cm long with 9 newly transplanted *Lithophaga plumula* as taken on 2 May 1979. As can be seen, X-rays of relatively thin shale show the shells of the experimental animals very clearly. Figure 2 is an X-ray taken exactly one year later. Six of the nine *Lithophaga* had survived and were alive, but none of them had grown by a measurable amount and only number 4 from the left had deepened the burrow. In all shale panels containing *Lithophaga*, as well as those containing *Adula falcata* and *A. californiensis*, the results were much the same. After one year the surviving *Lithophaga* had secreted a calcareous lining to the artificial burrow and a perforated conical plug at the exposed end. They therefore fitted more snugly in the burrow than when it was cylindrical. Several of these shale panels will be kept under observation for an additional extended period of time to see if ultimately the animals increase in size and extend the burrows. Subtidally off Monterey in shale of the same hardness as the experimental panels, *Lithophaga* commonly are 55 mm long. The largest experimental animals (Figures 1 and 2) are 45 mm long.

As previously mentioned, of the pholads only *Penitella penita* and *Chaceia ovoidea* survived transplantation and lived for extended periods of time. Immature specimens of experimental *P. penita* from the intertidal shale at Santa Cruz averaged 25 mm in shell length, and 14 mm in shell diameter. These were introduced into artificial burrows that averaged 52 x 15 mm in size. After 9 months of exposure in racks in the intertidal zone in Monterey the animals that survived had grown to an average shell length of 50 mm and diameter of 23 mm, and the burrow had increased to an average depth of 75 mm and diameter of 23 mm. The bimonthly X-rays showed a rather steady growth in shell length (averaging 2.8 mm per month) and a deepening of the burrow (averaging 2.6 mm per month) until about the ninth month when the animals ceased to grow and burrow, and underwent metamorphosis with the formation of a callum over the anterior pedal gape.

EVANS (1968c) found that *Penitella* in natural stone substrate at Fossil Point in Oregon had boring rates of 50 mm per year and when animals reached a shell length of 55 mm (after about 3 years from larval settlement) they metamorphosed. In experimental shale panels of about the same hardness as the rock at Fossil Point, *P. penita* in Monterey grew to about the same shell length before

metamorphosis, but the average animal had a boring rate of only about 31.2 mm per year (2.6 mm per month).

Of all the pholads studied in this investigation, *Chaceia ovoidea* proved to be most adaptable when transplanted to artificial burrows and most of the transplants survived, underwent growth, and burrowed deeper until they had exhausted the space for additional growth and burrowing.

In Monterey Bay, *Chaceia ovoidea* lives in the intertidal shale in the reefs at Santa Cruz. Most specimens that can be collected from the reefs are small, up to 17 mm in shell length. All are immature, and no large animals are found, indicating that severe erosion exposes and destroys the animals before the long-lived borers become mature. In subtidal shale off Monterey, however, mature *Chaceia* commonly are found with a shell length of 115 mm and a diameter of 70 mm. These large animals have a long siphon and can form burrows in the shale 60 cm or more deep (HADERLIE, MELLOR, MINTER & BOOTH, 1974).

An indication of the rapid burrowing rates of *Chaceia ovoidea* was obtained when one thick shale block of a hardness similar to the shale used later in the X-ray studies was exposed in Monterey harbor in May 1975 and recovered for analysis a year later in May 1976. In addition to a few other pholads, this shale had been penetrated by one individual *Chaceia*. The shale block had distinct bedding planes so it was carefully split open along a bedding plane that contained the *Chaceia*. This resulted in a longitudinal section of the *Chaceia* burrow and the animal could be removed and measured. The pholad had settled sometime during the previous year and in May 1976 had a shell length of 40 mm and a diameter of 30 mm; the bore hole was 137 mm deep with an entrance diameter of

12 mm and a basal diameter of 32 mm. This animal had bored at a rate of at least 11.4 mm per month during this first year. After measurements were complete the *Chaceia* was returned to its burrow, the two pieces of shale fitted back together and bound with elastic bands, then the shale block was returned to the rack in the water. This specimen was retrieved and examined monthly and in general the increase in shell length over several months ranged from 1 to 3 mm per month. By September 1977 the animal had bored to the point where it was about to break through the distal edge of the shale block with less than 10 mm of stone remaining. It then ceased boring and formed a callum over the pedal gape. The shell valves at this time were 60 mm long and 40 mm in diameter. The burrow was 302 mm long and had an entrance diameter of 20 mm. This animal was therefore under observation for some 15 months and during that time had increased in shell length from 40 mm to 60 mm. It had increased the burrow depth from 137 mm to 302 mm. The soft siphons had in some way increased the diameter of the entrance hole from 12 to 20 mm in the 15 month period. The animal was kept in its burrow in the shale and was still alive in January 1979, but when examined in June 1980 it had died and only the shell valves remained.

Since May 1979 ten experimental *Chaceia ovoidea* in artificial burrows have been under observation using X-ray techniques. The shale used was of the same hardness as that employed in studying the growth rates of *Penitella penita*. The *Chaceia* used in these studies were all obtained as juveniles from subtidal shale off Monterey and varied in size from those with shells 15 mm long to others 35 mm long. Once transplanted to the artificial

Explanation of Figures 1 to 10

Figures 1 to 10 are X-ray photographs of boring mytilids and pholads in shale panels or blocks. The scale on the top photograph applies to all figures on that plate

Figure 1: X-ray photograph of shale panel with 9 *Lithophaga plumula* in artificial burrows, 2 May 1979

Figure 2: Same panel as shown in Figure 1, one year later, 2 May 1980. Three of the bivalves had disappeared, and although they were alive, none of the others had grown in shell length in one year

Figure 3: X-ray photograph of shale block with 2 *Chaceia ovoidea* in artificial burrows, 2 May 1979

Figure 4: Same panel as shown in Figure 3, 3 July 1979. The upper animal had increased the burrow length by 26 mm, the lower one (seen dimly) had increased its burrow length by nearly 30 mm

Figure 5: Same panel as in Figure 3, 2 September 1979. The animal at top had moved part way out of the burrow and had not increased the burrow depth. The lower animal had grown and deepened the burrow considerably

Figure 6: Same panel as in Figure 3, 9 November 1979. Upper animal had dropped out of the burrow and disappeared. Lower one continued to grow and to extend the burrow

Figures 7 to 9: X-rays of the same panel as in Figure 3 taken on 2 January, 4 March, and 2 May 1980. The one remaining *Chaceia* had continued to grow and to extend the burrow

Figure 10: Terminal X-ray photograph of panel, taken 1 July 1980. The animal had ceased to grow and burrow and only 5 mm of stone remained between the end of the burrow and the edge of the shale



Figure 1



Figure 2

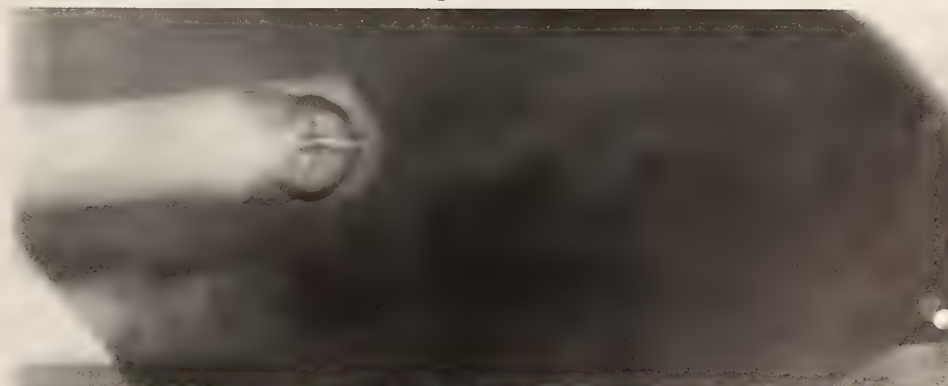


Figure 3

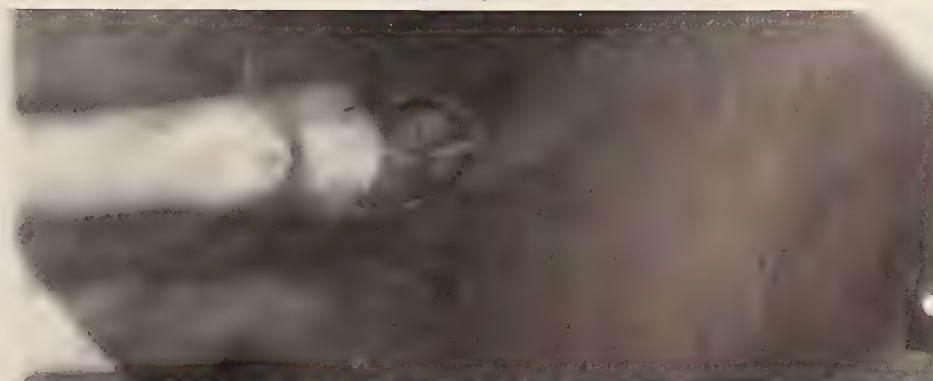


Figure 4



Figure 5

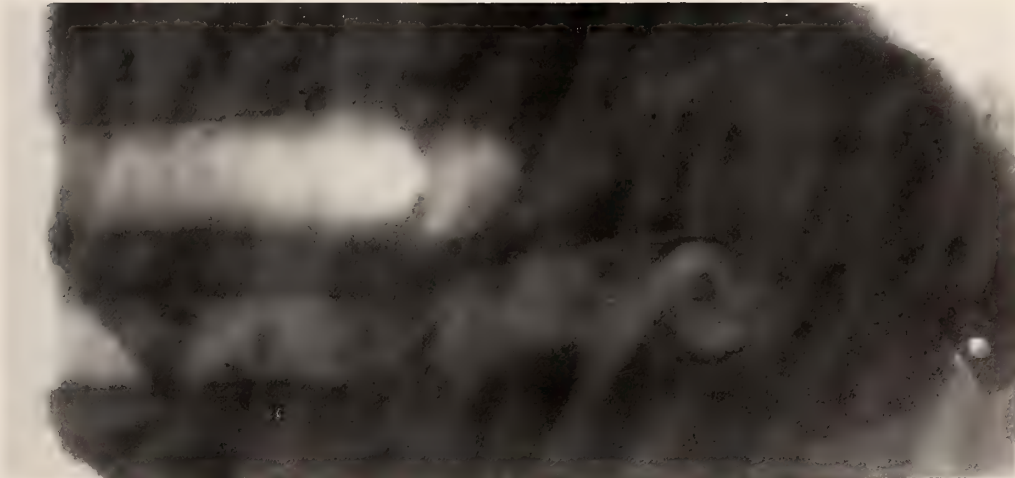


Figure 6



Figure 7



Figure 8



Figure 9



Figure 10

burrows the animals adapted well, although there was some mortality. The experimental shale blocks containing *Chaceia* were all exposed in racks suspended just above the bottom in water 7 m deep. Most of the animals that survived transplant grew at about the same rate.

In order to give the young *Chaceia* ample room for growth they were transplanted to rather large thick pieces of shale; a typical block measured 26 cm long, 16 cm wide, and 14 cm thick. It was, therefore, difficult to get really clear X-ray pictures of the animals in the thick shale. Figures 3-10 are a series of the better X-rays obtained and show typical growth and burrowing rates. Figure 3 shows two *Chaceia* in place in artificial burrows on the day they were transplanted. The animal on the top had a shell length of 35 mm, a diameter of 25 mm; the one on the bottom a shell length of 27 mm, a diameter of 20 mm. Although all burrows were plugged with perforated corks, the powerful siphons of even small *Chaceia* soon pushed the corks out. Figure 4 shows the two borers after two months' exposure in the sea. The animal on the top had increased its burrow depth by 26 mm, the animal on the bottom by 30 mm. In Figure 5 two months later, the animal on the top had not bored any deeper, but had moved outward in the burrow and had its siphons extending some distance out of the entrance hole. The animal on the bottom had now extended its burrow to a depth of 155 mm, an increase in depth of 50 mm in two months. This animal had increased its shell length from 29 mm to approximately 40 mm in the same period. Figure 6 shows that the *Chaceia* on the top was now gone (for unknown reasons) and the remaining animal had extended the burrow by an additional 28 mm in 2 months. Figures 7-9 show additional periods of growth and tunnel excavation.

By May 1980, one year after being introduced into the burrow, the *Chaceia* shown in Figure 9 had increased in shell length from 27 mm to 55 mm, and in diameter from 20 mm to 42 mm. The initial burrow depth was 60 mm; at the end of one year it was 250 mm. Figure 10 shows the animal about at the same position and depth as two months earlier. Only 5 mm of stone remained between the end of the burrow and the edge of the shale and no additional burrowing was possible. After making the final X-ray, the panel was broken and the animal recovered. The shell size was about the same as had been determined by X-ray two months earlier, and the animal was still in the boring stage with no evidence of a callum. The live pholad was then placed in a flat bottomed glass jar that fitted it reasonably well and returned to the subtidal exposure site. After a month it had formed a rather wrinkled yet fairly normal shaped callum. Thus, *Chaceia* appears to form a

hemispherical callum regardless of the shape of the blind end of the burrow at the time of callum formation. This is in contrast to what has been observed in the case of *Penitella penita* where the shape of the blind end of the burrow determined the shape of the callum (HADERLIE, 1981).

As noted earlier, except for *Penitella penita* and *Chaceia ovoidea*, the mortality rate for transplanted pholads was so high that despite repeated transplants we achieved little success in keeping animals alive for any extended period of time and therefore have little information on growth rates. The few data we have collected will be briefly reviewed below.

Penitella gabbii: The longest period of time any individuals of this species were kept alive in artificial burrows was 6 months and in all cases growth in these burrows was slow, averaging an increase in burrow depth of less than 1 mm per month. In shale blocks exposed on the bottom in Monterey harbor in October 1974, *P. gabbii* was one of the most common pholads to settle and penetrate the stone. By October 1977 many specimens with shells up to 30 mm long were removed from the shale. The largest of these had a newly formed callum. Thus, in burrows of their own making *P. gabbii* can grow in shell length by 10 mm or more per year.

Parapholas californica: A few individuals of this species were kept alive in shale burrows for up to one year but only one increased in size and extended the burrow depth. This animal increased in shell length from 25 mm to 30 mm in one year and had extended the burrow from 35 to 50 mm in depth.

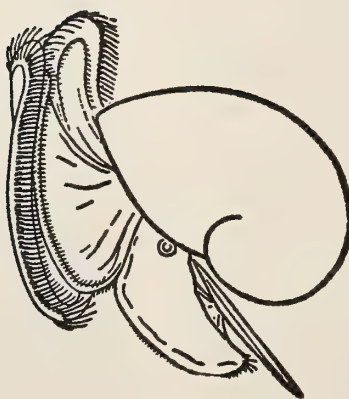
Netastoma rostrata: None of the *N. rostrata* transplanted to artificial burrows survived the process, for the shell valves of this species are particularly fragile. In shale samples submerged in Monterey this small pholad settles throughout most months of the year. After breaking apart shale that had been submerged for known periods of time we gained some data on growth rates. After one year many *Netastoma* were 12 mm long, including the tapering siphonoplax. After two years the largest were 25 mm in overall shell length.

As noted earlier and illustrated in Figures 1 and 2, mytilids survived well in artificial burrows, but none showed any growth in shell length after as much as 18 months following transplantation. Yet many specimens of *Adula falcata*, *A. californiensis* and *Lithophaga plumula* remained alive and the latter often formed calcareous linings to their artificial burrows. In shale exposed on the bottom in Monterey *Adula falcata* settled and some specimens were 18 mm long after the stone had been in the water

2 years. *Lithophaga* also settled and achieved a shell length of 24 mm in stone exposed for 2 years. Rates of growth cannot be determined, for the exact date when the larvae settled was unknown.

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Shell Shape Changes in the Gastropoda:

Shell Decollation in *Rumina decollata*

(Pulmonata : Subulinidae)

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(1 Plate; 3 Text figures)

INTRODUCTION

CHANGE IN SHELL SHAPE with increasing size is a common phenomenon among the Gastropoda. Shape changes are always evident when larval and juvenile shells are compared, but, more interestingly, such changes may also occur when the gastropod reaches the adult stage (the terms "juvenile" and "adult" are used herein to describe shell shape: they do not necessarily correspond to reproductive maturity). Basically, these further changes are mediated by three main processes, alone or in combination: alteration of coiling patterns, reorganization of, and addition to existing shell material. Alterations in the pattern of coiling are perhaps best illustrated by the Vermetidae, in which the initial shape is turritiform, but frequently becomes erratically sinuous as growth proceeds with a progressively more uncoiled shell. Reorganization of shell material with alteration of coiling is found among the Cypraeidae, in which an initially elongate, spindle-shaped shell is at least partially resorbed once the outer, dome-shaped adult shell is formed over it (BERNER, 1942). Addition to existing shell material is found among a number of families, and usually involves strengthening of the outer lip. Overall shell shape is perhaps most affected in the Strombidae and the Aporrhaidae, where adults are characterized by a wide, flaring lip. The gastropod shell is thus far from limited to a shape dictated by the generating curve of coiling, but can be manipulated to a large extent during the life of the animal (BERNER, 1942; VERMEIJ, 1970). It has generally been accepted that such shape changes are adaptive: external additions of shell material are considered stabilizing and/or antipredatory, for example (VERMEIJ, 1977).

It is my purpose to document the effects of a fourth process, decollation, whereby an appropriately named land snail, *Rumina decollata* (Linnaeus, 1758) is able to effect a change in shape from a turritiform juvenile shell to a roughly cylindrical adult shell. Decollation of the upper whorls by *R. decollata* was described as early as 1759 by Brisson (VIGNAL, 1919). Subsequent authors restricted themselves to anecdotal observations on the process of decollation and life history without mention of the effects of growth changes on shell shape and associated advantages. Decollation is often encountered (and is probably of polyphyletic origin) among turritiform land snails (*e.g.*, *Truncatella pulchella* Pfeiffer, 1839, *Chondropoma dentatum* (Say, 1825), *Opisthosiphon bahamensis* (Pfeiffer, 1865), *Cochlodinella poeyana* (Orbigny, 1841)), rarely among marine snails (*e.g.*, Caecidae), and has not been reported for freshwater snails. To my knowledge, *Rumina decollata* is one of the largest and most common species in which this process occurs, and demonstrates clearly the large effect a rather simple modification of growth can have on the overall shape of a gastropod shell.

METHODS

Snails were collected on or among clumps of soil or on vegetation in gardens of the Urbanizacion El Rosario, ca. 7 km east of Marbella, Malaga, Spain. Densities were highest under moist matted vegetation; adults were also found in more xeric conditions under low bushes and rocks. Soils in the area contain high levels of calcium derived from the carbonate formations of the Sierra Blanca, a coastal range behind Marbella.

Juvenile and adult total shell length, and length and width of the body whorl were measured with Vernier calipers; foot length was measured on live animals crawling on glass. Whorls on the dorsal side were also counted. Shells were prepared for SEM by soaking briefly in dilute Clorox, ultrasonicing, and finally drying for 24 hours at 60°C.

RESULTS AND DISCUSSION

The juvenile shell of *Rumina decollata* is turritiform in shape, and is capped by a dome-shaped larval shell (Figure 1D). Growth proceeds until 8 or 9 whorls are present on the shell, after which a septum is formed below the 3rd or 4th whorl, and the body withdrawn into the remainder of the shell. Of those specimens found with a maximum of 9 whorls, no more than 15% ($n=13$) occupied the entire shell. The remainder had already formed the initial septum, but the top part of the shell remained partially attached. Those with 8 whorls ($n=18$) had formed septa above whorls 4 and 5 with a frequency of about 40%. Juveniles with fewer than 8 whorls had not formed septa.

The adult shell (Figure 1A) bears little resemblance to that of the juvenile. With decollation of the upper whorls, the top of the shell has become flattened, and the overall shape is now cylindrical. No more than 6 whorls are ever present on the adult shell, with the number decreasing to 5 or 4 as the animal increases in size. It is evident that new septa are laid down at regular intervals, possibly as soon as a maximum of 6 whorls is present.

The effects of this reduction in shell length mediated by decreasing the number of whorls present on the shell are illustrated in Figures 2 and 3. Shell length at first increases linearly as successive whorls are added to the shell. When 8 or 9 whorls are present, and the initial septum deposited, shell length decreases as the top sections are decollated. Further increase in length then becomes decoupled from the number of whorls on the shell (Figure 2). When shell

length is plotted against width of the body whorl, juveniles cluster tightly and fall on a line statistically different from that of adults (F test for comparison of regression lines, $p < 0.01$) (Figure 3). When the juvenile reaches a maximum length of 15.5 mm, further increase in shell width begins with a shorter shell. The increase in the spread of

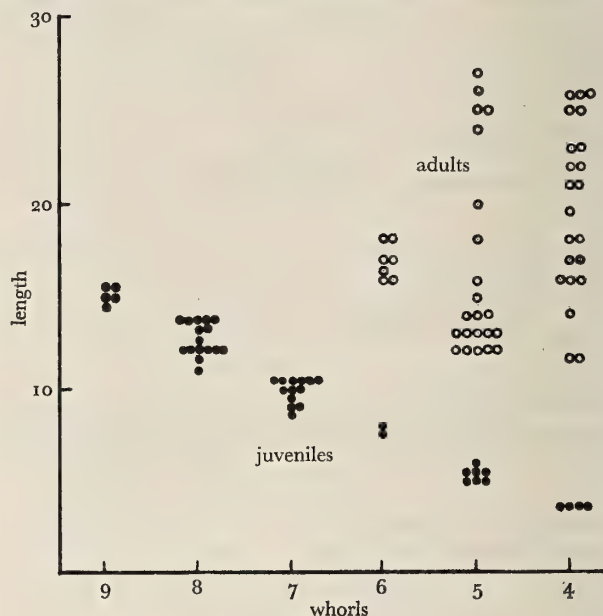


Figure 2

Increase in shell length with whorl addition in juveniles, and the lack of this relationship among adults

points about the regression line for adults is due to the fact that increases in adult shell length are less correlated with increases in shell width: shells with the same width may have 4, 5 or even 6 whorls. Decollation of the upper whorls thus allows increases in the size of the body whorl without increasing shell length.

Explanation of Figure 1

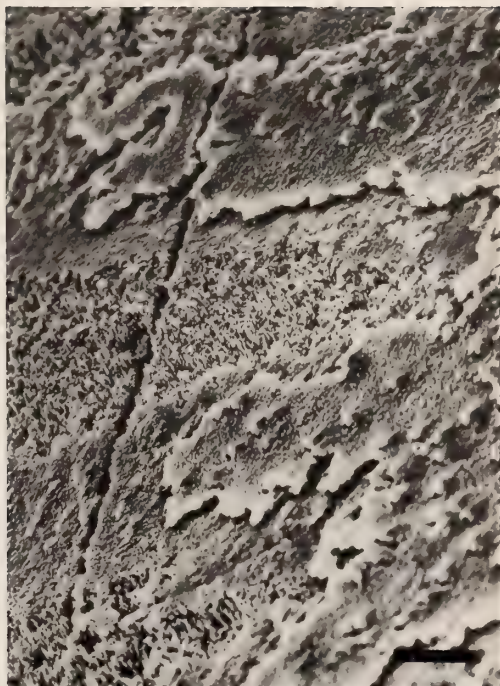
- A. Decollated shell of an adult *Rumina decollata*. Scale bar = 5 cm
- B. Shell edge of a decollated whorl. Note the rounded appearance of the shell crystals at the bottom of the picture. Scale bar = 30 μ m
- C. Interior wall of a shell whorl above a septum. Scale bar = 20 μ m
- D. Shell of a juvenile *Rumina decollata*. Scale bar = 200 μ m



a



b



c



d

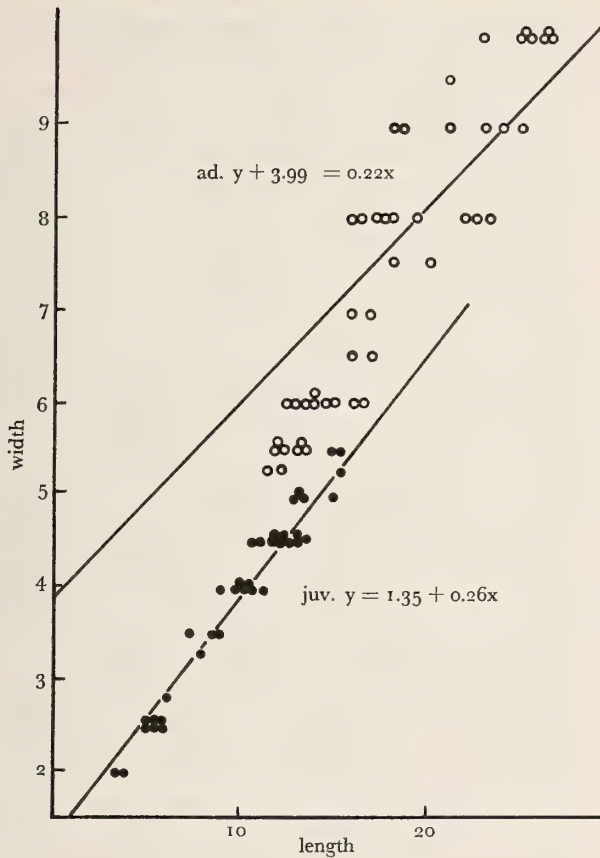


Figure 3

A plot of shell length against width of the body whorl in juveniles and adults

It is not clear why the initial septum is not formed until the animal has already laid down 8 or 9 whorls and measures from 13.5 to 15.5 mm in length. Examination of non-decollating turritiform land snails, however, reveals that the maximum adult size averages around 14 mm (PILSBRY, 1946). It would be intriguing to examine this apparent size limit further to determine if it is physiologically and/or mechanically determined.

When shell length is plotted against foot length (Figure 4) juveniles and adults again fall on different regression lines ($p < 0.01$). Decollation of the upper shell whorls thus allows increases in foot size without the necessity of having

to transport and support an increasingly elongate turritiform shell.

It is interesting to note that juvenile and adult regression lines intersect at a point where the juvenile shell has 4 to 5 whorls, roughly 3 of which represent the larval shell (Figure 4). It is at this point that juvenile and adult shells most resemble each other: both are rather squat and flat-topped, and hence far from the turritiform shape of the older juveniles. VIGNAL (1919) finds a resemblance between young *Rumina* juveniles and *Pupa* sp., and mentions that at one time each developmental stage had separate species status: *R. decollata* (adults), *Orbitina incomparabilis* Risso, 1826 (juveniles) and *O. truncatella* Risso, 1826 (young juveniles).

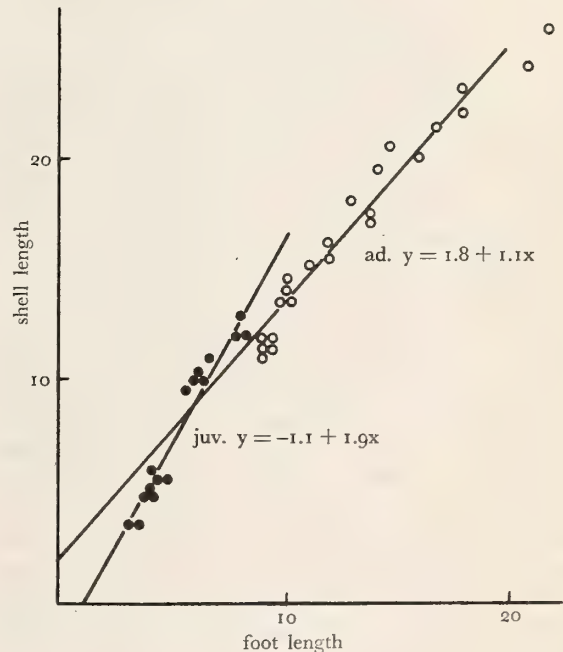


Figure 4

A plot of foot length against shell length in juveniles and adults

Terrestrial gastropods, much more so than marine or aquatic forms, have severe restraints placed on the weight of their shell. Shells are probably thin not only due to difficulties in obtaining calcium in some habitats, but also because of the energetic expense involved in transport of

the shell. Selection against such expense is probably balanced by anti-predatory selective forces which drive towards a thicker, or at least a more structurally resistant shell. Due to its design, a turritiform shell is heavier than a discoid or turbinatate shell of the same aperture size with a greater whorl expansion rate (e.g., *Helicella*, *Cepaea*, but not *Polygyra*, *Stenotrema*). Decollation of the upper whorls not only reduces shell weight, but also increases structural resistance: the thickest sections of the shell are retained, and the truncate shell may be measurably more resistant to shear forces exerted by predators.

It is important to point out that decollation is an adaptation which alters shell shape secondarily. The animal has to deposit a similar or larger (due to septum formation) amount of shell material as does a snail which retains a turritiform shell. Calcium is thus not conserved by this adaptation, even though the animal carries a shorter and lighter shell. Both BERNER (1942) and VIGNAL (1919) mention, however, that the portion of shell above the septum is very thin walled, and may have been partially resorbed. Vignal also mentions that before withdrawing into the remaining portions of the shell, the animal secretes a substance which corrodes the shell above the septum to facilitate decollation. I am unable to confirm this observation except to note that those specimens which retained old whorls always exhibited an elongate hole just above the septum, also observed by FRÖMMING (1956), where shell material may have been dissolved away. Examination of the edges of this hole with an SEM reveals that the shell crystals are indeed rounded and may have been corroded (Figure 1B), but whether this is part of a normal weathering process or due to substances secreted by the animal could not be determined. The thickness of the whorls about to be cast off is indeed less than the remaining whorls, and examination of the interior walls with an SEM (Figure 1C) reveals the unmistakable signs of resorption of shell material (e.g. LUTZ & RHOADS, 1977), confirming the observations of Berner and Vignal. This resorbed calcium may be used in the formation of septa.

Mobility of terrestrial gastropods is strongly affected by shell weight as well as shell shape. When turritiform gastropods such as *Rumina* juveniles crawl on vertical surfaces, the shell is pulled down by gravity. If the body of the animal is parallel to the ground, the shell is oriented at almost right angles to the body. When the snail crawls down a vertical surface, the shell falls to the left of the body, and the tip extends well past the head. Gastropods with rounded shells do not share this problem: no matter how the animal is oriented, the tip of the shell never projects past the head, or far beside the body. Shortening a turritiform shell by decollation may reduce these disadvantages.

Terrestrial gastropods of semi-arid regions restrict their periods of activity to the coolest and wettest parts of the year. During the summer months, all gastropods aestivate. The shell is important in controlling rate of evaporative water loss, and is impermeable to water at normal temperatures (MACHIN, 1975). However, differences in shell thickness and surface area result in widely different total water losses during aestivation (MACHIN, 1975). Again due to its design, a turritiform shell has a greater surface area than a discoid or turbinatate shell of the same aperture size. Decollation of the upper whorls not only reduces surface area, but may also reduce evaporative loss directly by allowing the animal to withdraw into the thickest parts of the shell (FRÖMMING, 1956).

Land snails in general do not assume a turritiform shape, in contrast to gastropods in both marine and aquatic habitats. The most common shape among terrestrial gastropods is discoid or turbinatate (Table 1). Among the elongate shells, perhaps the pupate forms most closely resemble turritiform shells in shape, but only as adults: juveniles are more trochiform (e.g., *Cerion*). Those truly turritiform in shape share several characteristics: they are rather small even as adults, often decollate the upper whorls, and seem to have habitat preferences for moist, protected environments (e.g., leaf mold, undersides of rocks, etc.) (PILSBRY, 1946; EMERSON & JACOBSON, 1976).

Table 1

Relative frequencies of land snail shapes
(calculated from PILSBRY 1939-1948 "Land Mollusca of North America")

Shape					
Turritiform	Triangular	Pupate	Turbinatate	Discoid	Decollated
4.3	6.9	12.5	38.5	36.3	3.6

Rumina decollata differs from most other turritiform terrestrial gastropods in adult size (up to 40 mm in length) and number of habitats occupied (SELANDER & HUDSON, 1976; FRÖMMING, 1956). It has a wide geographic range in Europe and North Africa, and is one of the most successful colonizing snails of the southern United States, Mexico, Bermuda and Cuba (PILSBRY, 1946; DUNDEE, 1970; SELANDER & KAUFMAN, 1973). Selander and Kaufman also note that *R. decollata* is regularly if not predominantly self-fertilizing. This could have led to rapid fixation of genetic combinations controlling decollation, which could conceivably have arisen in a single ancestral individual (it is interesting to note that septum formation is usually involved in shell repair: the process of decollation seems to differ little from this basic response, except that the septum is formed in an intact shell). It is my opinion that the resultant changes in shell shape delivered considerable selective advantages by virtue of increased mobility, shell weight reduction and resistance to desiccation. It is also conceivable that decollation allowed increases in body size (for reasons discussed above: the shell remains compact, regardless of body size) which may have led to increases in fitness over ancestral forms (because of the direct relationship between body size and fecundity in gastropods).

Shell decollation is thus comparable to other processes such as heterochrony (GOULD, 1977; STANLEY, 1979) whereby simple changes in genetic commands result in major changes in shape, size and ecology of the species involved.

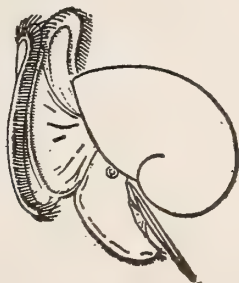
ACKNOWLEDGMENTS

My family aided immeasurably by collecting specimens from Marbella. Drs. Alan Walker and Pat Shipman and

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Two New Cryptobranch Dorid Nudibranchs from California

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(1 Plate; 12 Text figures)

INTRODUCTION

DURING COLLECTION OF BIOLOGICAL MATERIAL by Pacific BioMarine Laboratories, Venice, California, several undescribed species of nudibranchs have been found. Presented here are descriptions of two new species of dorid nudibranchs. We express our sincere thanks to Dr. Rimmon C. Fay, for the opportunity to collect these species.

Thordisa Bergh, 1877

Known worldwide, the genus *Thordisa* is represented by only one species in the northeastern Pacific. As with so many other cryptobranch dorid genera, the diagnostic characters of *Thordisa* are highly disputed (ELIOT, 1910; KAY & YOUNG, 1969; LANCE, 1966; MARCUS, 1955; MARCUS, 1967 a & b). If agreement exists, it centers around the presence of pectinate marginal teeth, hamate lateral teeth bearing no denticulation, soft elongate dorsal papillae, an unarmed penis and the absence of labial armature.

The first known collection of this previously undescribed species of *Thordisa* was made in October, 1973 (Rimmon Fay, personal communication). This specimen was photographed but not preserved. Additional collections have been made since that time.

Thordisa rubescens Behrens & Henderson, spec. nov.

(Figures 1 through 7, 13 and 14)

References and Synonymy:

Thordisa sp.: Behrens, 1980: 102.

Material examined: 1) Holotype: One specimen approximately 90 mm long live (67 mm long preserved) collected in 15 m of water, at Big Kelp Reef, Paradise Cove area, Los Angeles County, California (Lat. 34°00'02" N; Long. 118°47'02" W) on October 17, 1979 by Robert Henderson. This specimen is deposited in the collection of the Invertebrate Zoology Department, California Academy of Sciences (CASIZ), San Francisco, California (CASIZ Catalogue No. 015860). 2) Paratypes: One specimen (50 mm long preserved) collected in 19-22 m of water at Big Kelp Reef, Paradise Cove Area, Los Angeles County, California, on November 5, 1979 by Richard Rhode. The intact specimen has been deposited in the type collection of the U.S. Natural History Museum, Washington, D.C. (USNM Type Series, No. 749790). 3) One specimen (36 mm long preserved) collected in 10 m of water at Palos Verdes, Los Angeles County, California (Lat. 33°45'05" N; Long. 118°22'47" W) on August 28, 1978 by Richard Rhode. The dissected specimen and its mounted radula are also in the CASIZ collection, Catalogue No. 015861. 4) One specimen (40 mm long preserved) col-

lected in 22 m of water at Big Kelp Reef, Paradise Cove Area, Los Angeles County, California, on October 8, 1978 by Robert Henderson. This dissected specimen and its mounted radula have been deposited in the type collection of the Los Angeles County Natural History Museum, LACM Type Series 1948. Color transparencies of living specimens of *Thordisa rubescens* are on file at CASIZ (Nos. 3724 and 3725), LACM and Santa Barbara Museum of Natural History, Santa Barbara, California (SBMNH) (Nos. 0001SL, 0002SL and 0003SL).

Description: The living animals measured from 55 to 90 mm long; preserved they measured 36 to 67 mm in length. The body is typically doridiform, oval with a bluntly pointed tail which extends slightly beyond the notum (Figures 1 and 13). The notum is convex, highest along the midline, sloping gradually to the margins. The entire dorsal surface of the notum is covered with inflated papillae of various sizes and shapes (Figures 2 and 14). Many are blunt, some conical, while others are inflated at mid-length and terminate in a tapering point.

Notably larger papillae are dispersed evenly over the notum, not being concentrated in any one region. The papillae of living animals were observed to shrink to less than one half their original size after only a short confinement in the aquaria. Protruding spicules are not localized and may occur anywhere on the papillae (Figure 2). The notal spicules are straight or slightly curved smooth rods (Figure 2). More dense near the surface of the notum, they form a reticulating system deep into the notal tissue.

The anterior margin of the foot is rounded to angular in outline and bilabiate with a slight cleft (Figure 3). The foot margins are parallel, while the foot width is about $\frac{1}{2}$ to $\frac{1}{3}$ the body width. The labial tentacles are blunt

and digitiform, arising independently on either side of the mouth, about $\frac{1}{4}$ the foot width on either side (Figure 3a).

The body color is brilliant red-orange, closely approx-

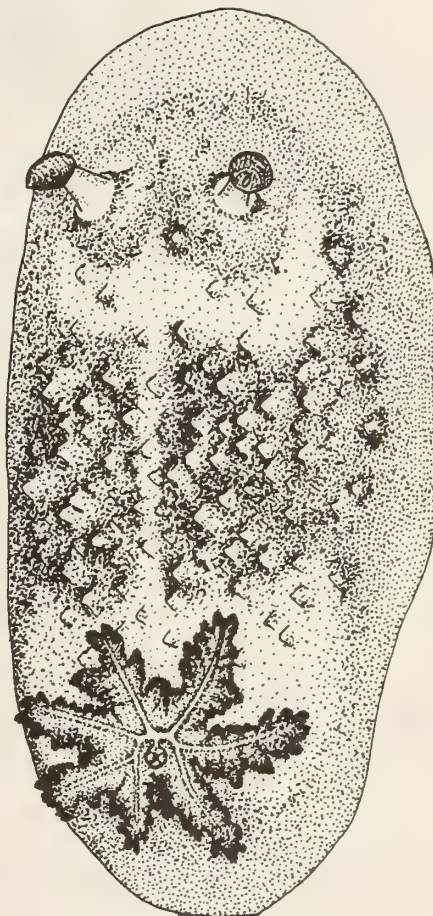


Figure 1

Dorsal and lateral view of *Thordisa rubescens*

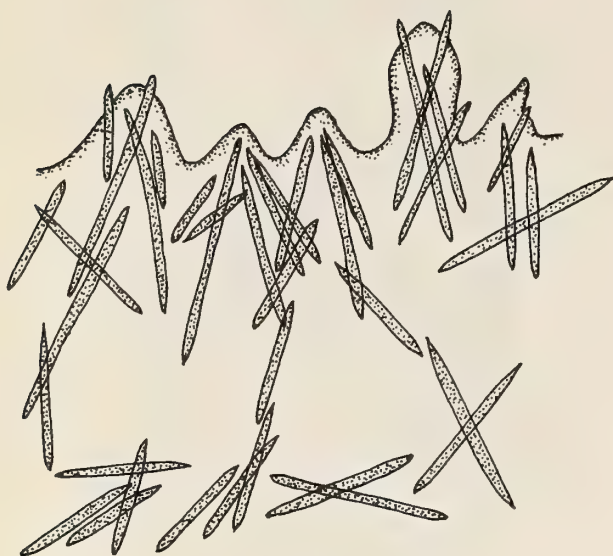
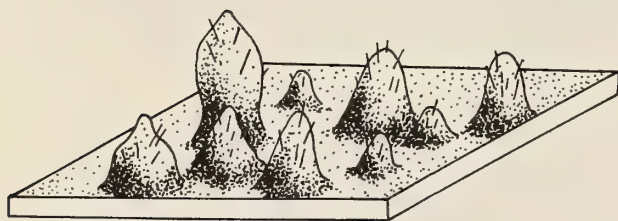


Figure 2

Plain and cross-sections of notal surface of *Thordisa rubescens* papillae and spicules

imating that of the substrate from which it was collected, the sponge genera *Axinella* and *Lissodendoryx*. The notum is encrusted with gold flecks forming a halo around the branchial pit, a mid-dorsal stripe and half crescents posterior to the rhinophores (Figures 4 and 14). The intensity of this pattern varies between individuals and, in fact, in two specimens was barely discernible. Accompanying the gold flecks may be black subcutaneous specks and opaque white surface flecks. Highly papillate specimens may have a black apical spot on some of the larger papillae. The rhinophore stalk is white to yellowish-orange. The clavus is orange to brown and has white flecks, scattered over its length, but more concentrated near the tip. The branchiae are lighter in color than the body, varying from white to orange below and centrally. They become brown near the

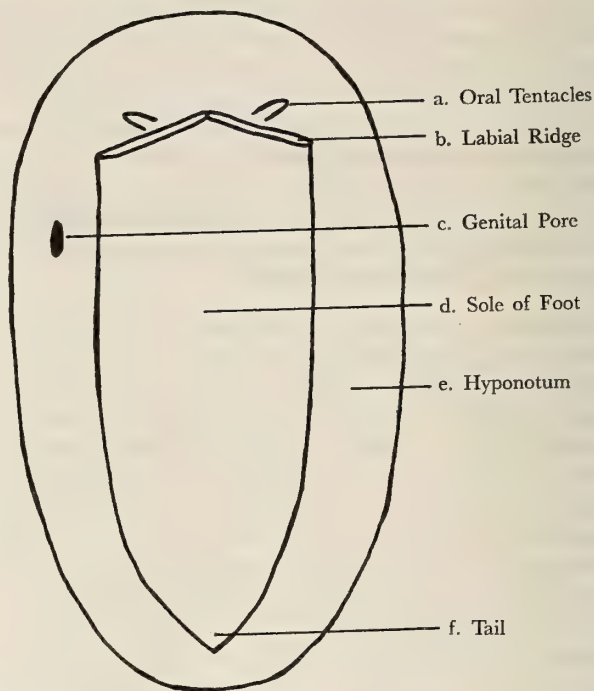


Figure 3

Ventral view of body of *Thordisa rubescens*

a - oral tentacles b - labial ridge c - genital pore
d - sole of foot e - hyponotum f - tail

tips. The upper surface of each gill is encrusted with brown flecks, upon which are larger, opaque white specks.

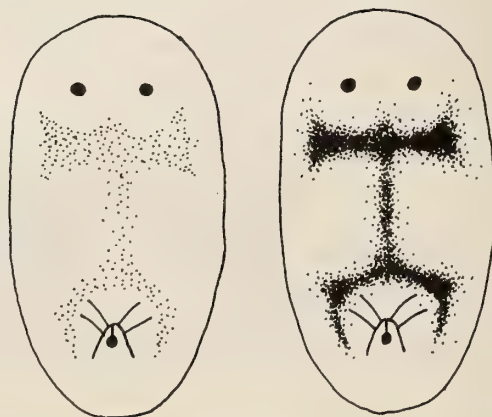


Figure 4

Schematic drawing of notal pattern in *Thordisa rubescens*

The edges of the branchiae are also highlighted with white flecks.

The rhinophores are long and retract into short, upright papillated sheaths. The stalk and clavus are equal in length. The clavus is deeply perfoliate with 20-21 diagonal lamellae. It has a shallow furrow along the anterior axis which terminates in a smooth, flattened tip.

The branchial plume is completely retractile into a branchial pit. The six bi- and tri-pinnate branchiae are upstanding and do not spread beyond the edge of the notum. The branchiae are joined by a horseshoe-shaped septum (Figure 5a), which is oriented posteriorly, encircling the anal papilla (Figure 5c). As in *Thordisa bimaculata* Lance, 1966 a characteristic septum (Figure 5b) connects the anterior side of the anal papilla to the horseshoe-shaped branchiae. The anal papilla is fluted distally into 5 lobes separated by 5 smaller lobes (Figure 5d).

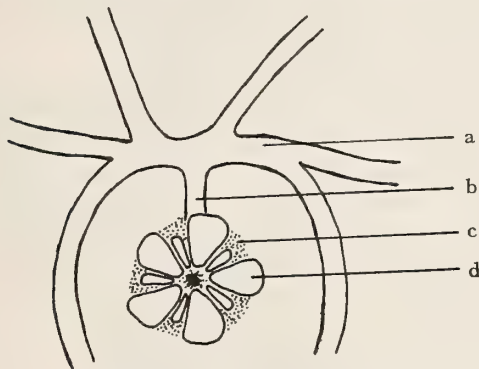


Figure 5

Branchial plume of *Thordisa rubescens*

- a - horseshoe-shaped septum connecting branchiae
b - connecting septum c - anal papilla
d - fluted margin of anal papilla

The radular formula is $39-40 \times 2 \cdot 39-40 \cdot 0 \cdot 39-40 \cdot 2$ at the 15th row. The innermost lateral teeth are small and hamate, increasing in size to the midpoint of the row, then decreasing again as they approach the edge of the radula (Figure 6a). The two outermost teeth are called marginals here, because of the distinctly different morphology compared to the laterals. The two marginals are bristled (Figure 6b & c). The innermost is hook-shaped, with a broad base (Figure 6c) and the outermost marginal is thin and as long as the anterior hook of the inner marginal (Figure 6b).

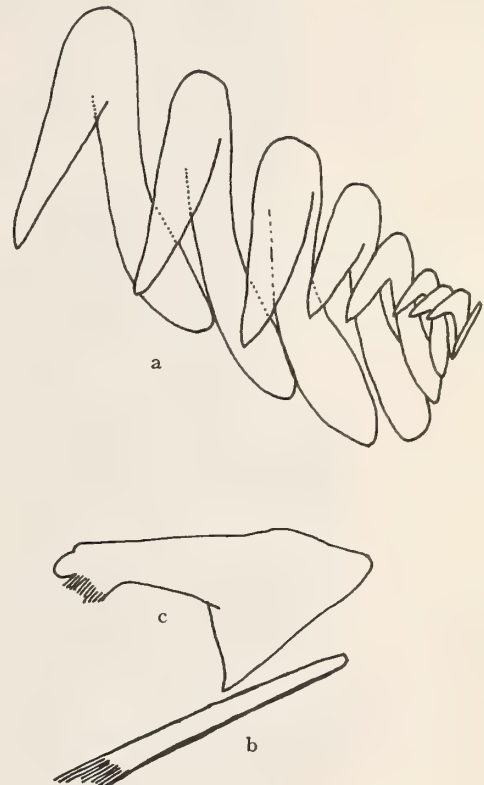


Figure 6

Radula of *Thordisa rubescens*

- a - lateral series, 27th row b - outer marginal tooth, 5th row
c - inner marginal tooth, 5th row

The genital opening is located on the right side of the body, just below the hyponotum and somewhat behind the rhinophores (Figure 3c). The vagina bears a series of spines, which are arranged both in a ring around the orifice and longitudinally within (Figure 7a). Each spine consists of a flat, opaque white disc having a single hook arising from its center (Figure 7b).

The egg mass is a pinkish-orange coil of two or three whorls attached to the substrate on one edge. The egg mass laid by the specimen collected October 8, 1978 measured 30mm in diameter, and 6mm in height. The ribbon was three eggs wide and 48-50 eggs high. Egg ribbons were encountered on red sponge, bare rock and on *Lithothamnion* encrusted rock surfaces.

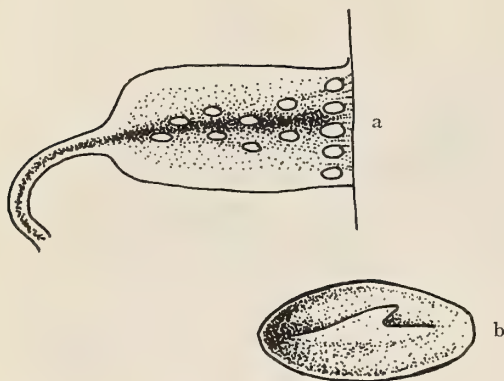


Figure 7

Genital armature of *Thordisa rubescens*

a - vagina, showing arrangement of spines

b - spine

Thordisa rubescens is known subtidally only. All specimens have been collected on or near the red sponges, *Axinella* and *Lissodendoryx*. The holotype was found living in, and covered by the slime of, *Lissodendoryx*. The only visible part of this cryptobranch was the branchial plume. Egg masses similar to those laid by the specimen collected October 8, 1978, have been observed on *Lissodendoryx*.

Discussion: Because of the radular morphology, this species is most closely aligned with *Thordisa*. MARCUS (1955:142) and MARCUS & MARCUS (1967:91) significantly reduce the number of species of known *Thordisa*, because of dissimilarities in radula to the type species, *Thordisa maculigera* Bergh, 1877, yet they state that the genus has been reduced too much. We assign *T. rubescens* here, in light of the similarities in radula and other characteristics known, to *Thordisa*.

Of the worldwide species of *Thordisa*, *Thordisa sanguinea* Baba, 1955 approaches *Thordisa rubescens* most closely, in external features. In *T. sanguinea* however, the

notum is marked with three or four dark ocelli along the midline. Internally, the radula of *T. sanguinea* adds to the differences having a formula of $30 \times 35 \cdot 0 \cdot 35$, five to six of the teeth at the margin being pectinate.

Thordisa rubescens, although strikingly distinctive, could be confused superficially with the other three red cryptobranch dorids in the northeastern Pacific. It most closely resembles *Aldisa sanguinea* (Cooper, 1863) particularly those individuals of *Aldisa* with the tan saddle marking. The external difference is the gill, *Aldisa*'s being cone-shaped with eight to ten unipinnate branchial plumes. Internally, the radular differences are pronounced. A second species, *Rostanga pulchra* MacFarland, 1905, rarely exceeds 16 mm in length. Of particular importance is *Rostanga*'s unique rhinophore; as in *Aldisa*, this and the radula are strikingly different from that of *Thordisa*. The third species, *Platydorid macfarlandi* Hanna, 1951 lacks the large notal tubercles, having a smooth notum with convoluted margins. The radula of this species lacks the pectinate marginal teeth.

It is distinguished from the only other member of the genus recorded in the northeastern Pacific, *Thordisa bimaculata*, by the number of rhinophoral lamellae, *T. bimaculata* having only 14-16; by the absence of the labial cuticle; by radular count, *T. bimaculata* being $32 \times 6 \cdot 8 \cdot 29 \cdot 34 \cdot 0 \cdot 29 \cdot 34 \cdot 6 \cdot 8$; and by color pattern (LANCE, 1966).

The specific (trivial) name *rubescens* is chosen to call attention to its red body color.

Jorunna Bergh, 1876

Jorunna has recently received a detailed review (MARCUS, 1976). Marcus lists 12 valid and 4 questionable species worldwide. This genus is previously unknown from the northeastern Pacific.

Jorunna is characterized by MARCUS (1976) by the following: stiffened notal tubercles, generally caryophyllidia; laterals simple, marginals sometimes with irregular denticles; prostatic epithelium smooth; male duct not

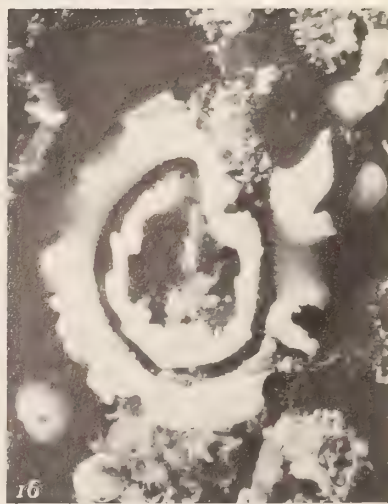
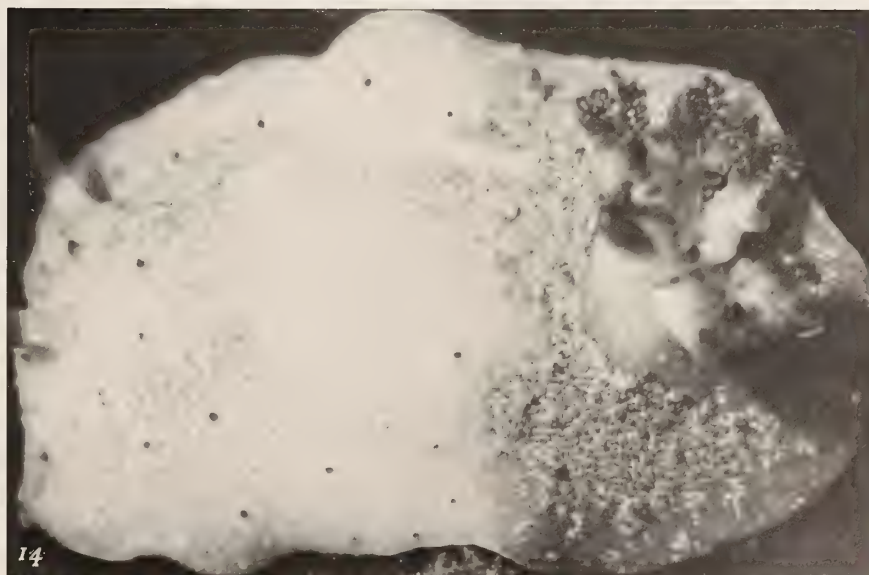
Explanation of Figures 13 to 16

Figure 13: *Thordisa rubescens*. Palos Verdes, Los Angeles County, California; 35 mm

Figure 14: *Thordisa rubescens*. Holotype. Big Kelp Reef, Paradise Cove area, Los Angeles County, California; 90 mm

Figure 15: *Jorunna pardus*. Cat Rock, Anacapa Island, California

Figure 16: Egg mass of *Jorunna pardus*. Bowen's Point, Santa Cruz Island, California



sheathed, ending with a papilla without a stylet, or even without a papilla; vestibular gland with a stylet.

This previously undescribed *Jorunna* is probably the most abundant cryptobranch dorid in the California "Channel Islands". First collected by James R. Lance in 1962, it has since that time been recognized as a major component of the molluscan fauna of the islands. In addition to the material collected by the authors, we are grateful to Jim Lance and Dave Mulliner for the use of their material and for their support towards this description.

Jorunna pardus Behrens & Henderson, spec. nov.

(Figures 8 through 12, 15 and 16)

References and Synonymy

Jorunna sp.: Behrens, 1980: 100.

Material examined: 1) Holotype: One specimen 45 mm long (preserved) collected in 5 m of water, at Cat Rock, Anacapa Island, California (Lat. 34°00'15" N; Long. 119°25'20" W) on October 25, 1979 by David W. Behrens. This specimen is deposited in the collection of CASIZ, Catalogue No. 015862. 2) Paratypes: A series of three specimens, 33, 35, and 35 mm long (preserved), collected concurrently with the holotype is also deposited in the CASIZ collection, Catalogue No. 015863. 3) A series of three specimens, 35, 37, and 38 mm long (preserved) collected concurrently with the holotype is deposited in the type collection of USNHM, Type Series No. 749791. 4) A series of three specimens, 25, 34, and 38 mm long (preserved) collected concurrently with the holotype is deposited in the type collection of LACM, Type Series No. 1949. 5) Two specimens, 30 and 34 mm long (preserved) collected in 15 m of water in La Jolla submarine canyon, San Diego County on October 7, 1975 by a USC dive class, are deposited in the type collection of SBMNH, Type Series No. 33599. Color

transparencies of living specimens of *Jorunna pardus* are on file at CASIZ (Nos. 3729 and 3730), LACM and SBMNH (Nos. 0005SL and 0006SL).

Description: The living animals measured up to 60 mm long (preserved, 45 mm). The body is typically doridiform,

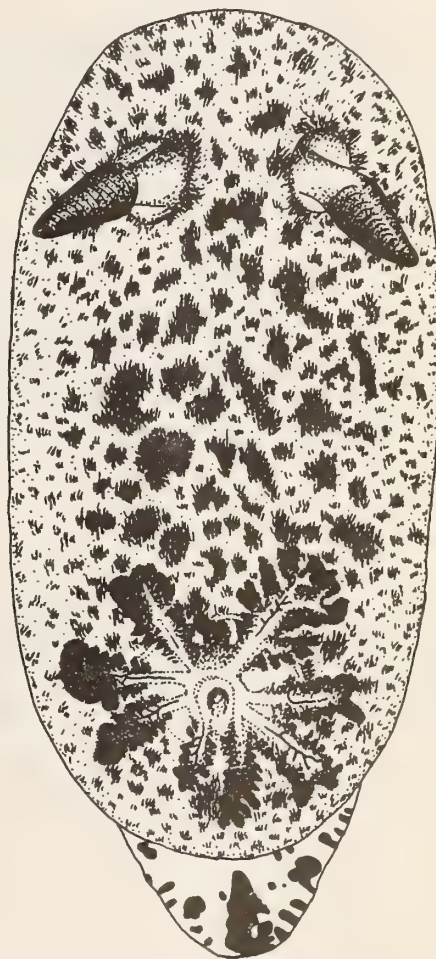


Figure 8

Dorsal and lateral view of *Jorunna pardus*

oval, with a bluntly rounded tail which extends beyond the notum (Figures 8 and 15). The notum is convex, highest along the midline, sloping gradually to the margins. The entire dorsal surface is covered with tall, bluntly rounded papillae (Figure 9a). Protruding dorsal spicules occur over the entire notal surface between papillae, as well as upon them (Figure 9b).

The spicules are smooth, straight rods, nearly 20 widths in length (Figure 9b). Near the notal surface, the spicules are perpendicular to the surface, while deeper in the notum, they are dispersed more randomly. Within the papillae, they are tightly packed, and form a radial pattern when viewed dorsally (Figure 9c).

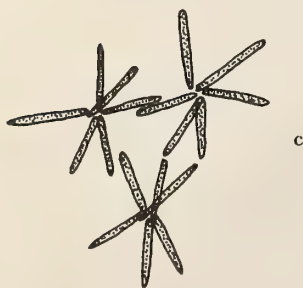
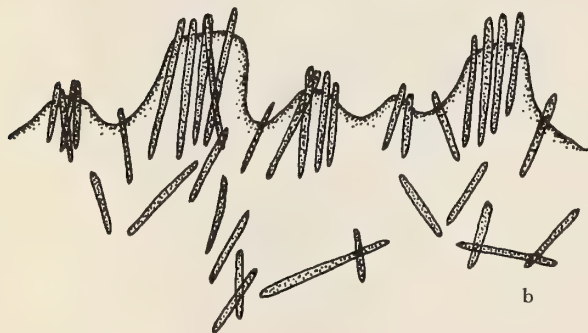
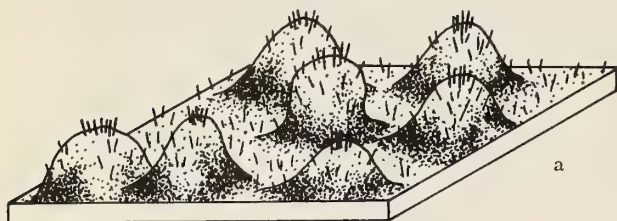


Figure 9

Notal surface of *Jorunna pardus*

a - plain view b - cross section c - dorsal aspect of spicules

The anterior margin of the foot is truncate and bilabiate (Figure 10). The foot margins are parallel and the foot is about $\frac{2}{3}$ the width of the body. The labial tentacles arise independently and are very long, tapering to a point. In preserved specimens, foot length is about 6 times the width (Figure 10).

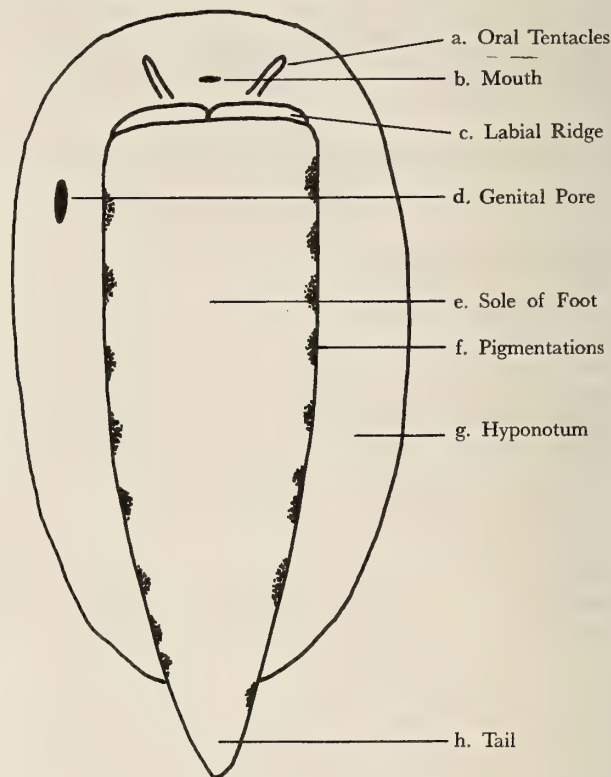


Figure 10

Ventral view of body of *Jorunna pardus*

a - oral tentacles b - mouth c - labial ridge
d - genital pore e - sole of foot f - pigmentation
g - hyponotum h - tail

The body color is cream to yellow with brown to black pigment concentrated into leopard-like spots (Figures 8 and 15). The spots vary in size. In some specimens, denser spotting gives the appearance of darker coloration. This is due to the existence of finer specks distributed between the larger spots. The dark color pigments may cover an individual papilla or be restricted to its base or even the periphery of the base. No such spotting exists on the hyponotum or the upper portion of the sides of the foot. The margin of the foot, however, has a series of similarly col-

ored spots which increase in size on the tail. The spots are visible through to the sole of the foot (Figure 10f). Rhinophore stalks are white to cream in color. The clavus is dark purple to black; however, the lower three or four lamellae are the same light color as the stalk. The interior surfaces of the branchial pits are lighter in color than the body. In some specimens, this color may approach white. The bases of the branchiae are similar in color to the body, while distally the branchiae are dark purple to black.

The rhinophores are long and can be retracted into sheaths level with the notum. The stalk is shorter than the clavus. The clavus is perfoliate with 15-17 diagonal lamellae. Separated by a cleft posteriorly, the lamellae bear a shallow furrow anteriorly and terminate in a smooth flat cap.

The branchial plume is completely retractile into a branchial pit. The eight bi- and tripinnate branchiae are upstanding and do not spread to the edge of the notum. The anal papilla is situated centrally within the branchiae.

The radular formula is $21\cdot42 \times 2\cdot23\cdot30\cdot0\cdot23\cdot30\cdot2$ at the 15th row demonstrating wide variation between specimens. The lateral teeth are hamate, the largest being at the midpoint of each half row (Figure 11). The two outermost teeth are marginals, due to their significant difference in morphology, and bear a series of irregular denticles (Figure 11b). The number and shape of the denticles on each marginal vary within a single individual. A few marginal teeth bear a circular series of small denticles flanked anteriorly by a single spur.

The genital opening is located on the right side of the body. The male duct is without armature. The vestibular gland contains a long cuticular stylet (Figure 12b). When everted, the vestibule forms a large papilla, from which the stylet protrudes (Figure 12).

The egg mass is a white coil of 2 whorls attached to the substrate on one edge. An egg mass collected at Bowen's Point, Santa Cruz Island, California on October 23, 1979, measured about 30 mm in diameter and 7 mm in height (Figure 16).

Jorunna pardus appears most abundantly in the Channel Islands, especially Anacapa and Santa Cruz Islands. It has also been collected from San Clemente, and Catalina Islands and from California's South Coronado and Cedros Islands. On the California mainland, it has been collected in the Paradise Cove, Palos Verdes and Point Dume areas in Los Angeles County, and in the Point Loma and La Jolla areas in San Diego County.

Discussion: Marcus (1976) contrasts *Jorunna* with *Kentrodoris* and other cryptobranch dorids. Radular morphology, notal texture and armed vestibular gland

provide assignment to *Jorunna*. One of the eight described worldwide species has similar spotting on the notum. In that species, *Jorunna pantherina* Angas, 1864 from Aus-

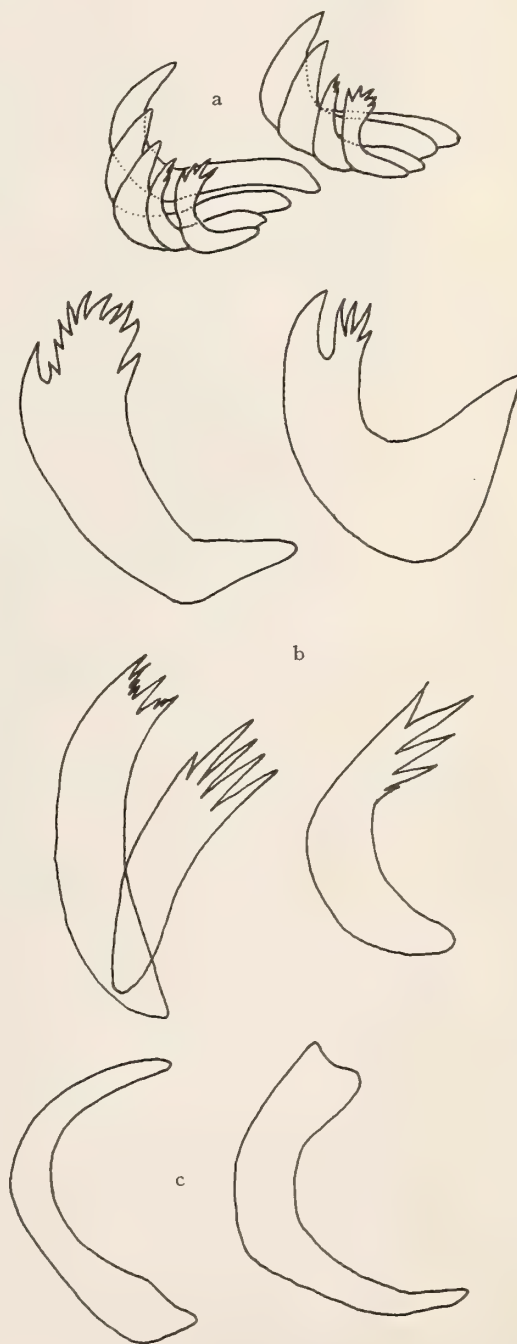


Figure 11

Radula of *Jorunna pardus*

a - lateral series

b - marginals

c - mid-row laterals

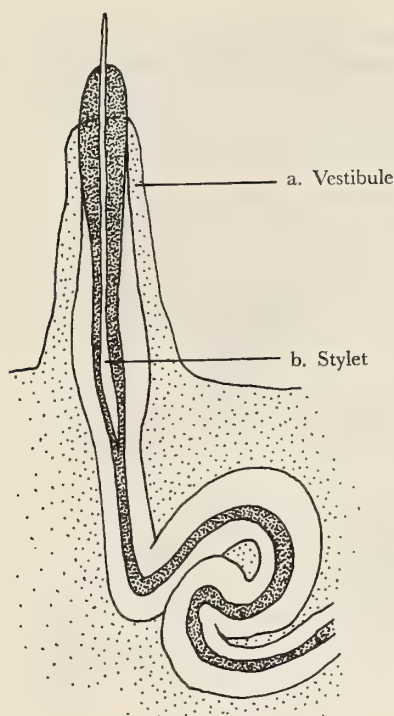


Figure 12

Vestibular gland of *Jorunna pardus*, everted with stylet protruding
a - vestibule b - stylet

tralia, the marginal teeth are not denticulate, and the rhinophores and gills are not dark. In two other species, *Jorunna funebris* (Kelaart, 1859) from Palau and the Philippines and *J. zania* Marcus, 1967 from Western Indian Ocean, the spots form rings. In these species, the marginal teeth are not denticulate as they are in *J. pardus*. ALLAN (1932) provides a color plate of a species which bears striking similarity to *J. pardus*. Named *Discodoris whitleyi* by Allan, KENNY (1970) eliminates it as a synonym of *J. funebris*.

Locally, *Jorunna pardus* might be confused only with an undescribed *Peltodoris* (BEHRENS, 1980:102). The *Peltodoris* sp., however, has yellow rhinophores and gill and large spots on the hyponotum.

The specific (trivial) name of *pardus* is chosen to call attention to the leopard-like spots on the notum of this species.

ACKNOWLEDGMENTS

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Feeding and Growth of *Octopus dofleini* (Wülker)

BY

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(3 Text figures)

INTRODUCTION

Octopus dofleini (Wülker) IS A LARGE OCTOPUS inhabiting coastal waters on the west coast of North America. MOT-
TET (1975) has reviewed some of the extensive literature on the fisheries biology of this octopus in Japanese waters. Although less is known about its habits on the west coast of North America, the potential of this octopus to support a limited fishery has been recognized (PENNINGTON, 1979; HARTWICK *et al.*, 1978a; R. Clifton, Washington State, personal communication). Field studies of *O. dofleini* on the west coast have included aspects of natural history and behaviour (HARTWICK *et al.*, 1978b, 1978c; KYTE & COURTNEY, 1977; HIGH, 1976a, b; JOHNSON, 1942) but relatively little is known of its feeding ecology and growth. Feeding and growth studies have been carried out for several other species of octopuses (see, for example, NIXON, 1966; VAN HEUKELEM, 1973, 1976; HANLON, 1977; JOLL, 1977; MATHER, 1980). Most of these studies have been restricted to the laboratory and the extent of such laboratory studies of one species, *Octopus vulgaris* Cuvier, is reflected in the recent book by WELLS (1978). Considerably less work has been done on octopuses in their natural environment, although there are exceptions (KAYES, 1974; HOCHBERG & COUCH, 1970; YARNELL, 1969; ALTMAN, 1967; WOODS, 1965). An indirect study of predation by octopuses has been reported (FOTHERINGHAM, 1974) but, in general, detailed information on feeding and growth under natural conditions is lacking.

The present study was initiated to obtain data on the feeding and growth of *Octopus dofleini* in its natural habitat. Aspects of diet and its variation were considered along with predator-size relationships. Short term growth experiments were also carried out and are discussed in relation to similar studies with other species.

MATERIALS AND METHODS

The study was carried out in Barkley and Clayoquot Sounds on the west coast of Vancouver Island, British Columbia. Information was gathered in 3 ways; collections of shells at octopus dens, tagging and recapture of octopuses in the field, and growth studies of captive octopuses.

Shells from octopus dens were collected from January through August, 1977, using SCUBA at 12 different sites within the 2 sounds. A total of 117 different dens was examined. After dens were located they were checked for prey items on a monthly basis from then on. Nine dens were checked at least weekly for more accurate information on feeding rates. Each collection of shells was accompanied by a record of the den site, its depth and date of collection. These factors were used in a multiple regression analysis to determine their relative contribution to the variation in the percentage of particular items in the diet. Significance was determined at the 5% level unless otherwise indicated.

To compare octopus size with prey size, the wet weights were estimated for 50 octopuses. This usually involved taking the octopus to the surface and obtaining a weight with a spring scale. In a few cases where an octopus escaped or remained in the den, its weight was estimated from the appearance of the octopus. This method was fairly accurate, although an error of 5 or even 10 kg might be expected in larger individuals. Prey items found at the dens were taken to the surface and measured with vernier calipers.

Although no quantitative estimates of prey availability were made, the presence and relative abundance of potential prey items were noted.

Information on the growth of octopuses was available through a tag and recapture program initiated in Clayoquot Sound in 1978. Individual octopuses were taken to the surface, weighed, sexed and then tagged with a Petersen disc at the base of one arm. These tags, commonly used

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on fish, were attached by inserting a pin through the arm. The tagged octopuses were taken back to their dens and released. In all cases tagged individuals moved back into their dens with no apparent effects from the tagging operation.

Additional information on growth and feeding came from experiments with captive octopuses. In July and August, 1977, 2 octopuses weighing 1.1 kg and 18.2 kg were placed in large aquaria (2.6 x 1.3 x 1 m) in running sea water in the Bamfield Marine Station at Bamfield, British Columbia. Observations were made on their feeding response to various freshly collected bivalves.

In October, 1978, 4 wild-caught octopuses were placed in running sea water (temp. 10-13°C) in separate aquaria (96 L tanks) at the marine station while 2 others were placed in a large partitioned box (117 L) with a plexiglass bottom and suspended from floats 1.5 m below the surface in Bamfield Inlet (Barkley Sound). The box had mesh-covered holes for water circulation. Surface temperatures in the inlet varied from 15°C in early October to 7.5°C in December.

The 4 octopuses in the aquaria were fed filleted hake, *Merluccius productus* (Ayres, 1855) and live kelp crabs, *Pugettia producta* Randall, 1839; just over 1% of body weight per day was made available. At times only hake or only crab was made available to see if the feeding rate was altered in comparison with that when both foods were available. Octopuses in the box suspended in the inlet were fed *ad libitum* on both *M. productus* and *P. producta* and also abalone *Haliotis kamtschatkana* Jonas, 1845 and the bivalves *Mya arenaria* Linnaeus, 1758, and *Protothaca staminea* (Conrad, 1837). The responses of the octopuses to these various food items were observed through the plexiglass bottom of the box. All remains were removed daily. All shells, crab exoskeletons and prey were weighed. Wet weights of octopuses were taken with a spring balance every 14 days. No anaesthetic was used during the weighing but the animals were suspended until excess water dripped off and gentle pressure was applied to remove water from the mantle cavity. Although some water undoubtedly remained in the mantle cavity the procedure was consistent with each octopus and was considered as minimum stress. Weighings of octopuses in the laboratory were less frequent than those in the box suspended in the inlet. Calculations of growth and feeding parameters were as follows,

$$\text{Daily growth rate} = \frac{W_2 - W_1}{tW} \times 100$$

$$\text{Daily feeding rate} = \frac{I}{tW} \times 100$$

$$\text{Food conversion} = \frac{W_2 - W_1}{I} \times 100$$

$$\text{Conversion ratio} = \frac{1}{\text{food conversion}}$$

where W_1 is the initial weight of an octopus, W_2 is the final weight, \bar{W} is the average weight over observation period t , and I is the weight of food eaten. The formulae come from NIXON (1966), VAN HEUKELEM (1973), JOLL (1977) and WELLS (1978). Food conversion is synonymous with food uptake (NIXON, 1966) and gross growth efficiency (JOLL, 1977).

RESULTS

DIET OF OCTOPUSES

Based on shell collections from dens in both Barkley and Clayoquot Sound, octopuses fed most frequently on bivalves and crabs. In particular, the cockle *Clinocardium nuttallii* (Conrad, 1837), the littleneck clam *Protothaca staminea* and crabs in the genus *Cancer* occurred frequently in the diet. The rest of the diet consisted of various molluscs and other organisms (Table 1).

The composition of shells at dens varied in both space and time. Regional differences showed up when collections from dens in Barkley Sound were compared with those from Clayoquot Sound. In Barkley Sound, the bivalve *Protothaca staminea* formed the greatest part of the diet (28%, $N=1478$) along with crabs, mainly *Cancer productus*, which accounted for 19% of the items at dens. Octopuses in Clayoquot Sound fed mainly on *Clinocardium nuttallii* (41%, $N=1014$) along with crabs (Figure 1).

In Clayoquot Sound, feeding on *Clinocardium nuttallii* remained generally high throughout the summer with increasing use of rock crabs, *Cancer productus* as well. The use of *Protothaca staminea* in this area remained relatively low throughout the study period. In Barkley Sound, feeding on the crab *C. productus* increased over the summer along with continuing dependence on *P. staminea*. In contrast to its heavy use in Clayoquot Sound, *C. nuttallii* appeared in only small numbers in dens in Barkley Sound.

There is evidence of individual differences in the feeding habits of octopuses. At times individual octopuses in the

Table 1

The diet of octopuses based on collections of shells at dens. Prey items are expressed as a % of total number (3492) of items found in all dens. Most are molluscs with other phyla indicated by superscript.

Prey item	%
<i>Clinocardium nuttallii</i> (Conrad, 1837)	28.81
<i>Cancer</i> spp.	27.0
<i>Protothaca staminea</i> (Conrad, 1837)	16.3
<i>Tresus capax</i> (Gould, 1850)	6.6
<i>Gari californica</i> (Conrad, 1837)	4.3
<i>Saxidomus giganteus</i> Deshayes, 1839	3.9
<i>Haliotis kamtschatkana</i> Jonas, 1845	2.8
<i>Chlamys hastata</i> (Sowerby, 1842)	1.5
<i>Macoma</i> sp.	1.4
<i>Polinices lewisii</i> (Gould, 1847)	1.1
<i>Hinnites giganteus</i> (Gray, 1825)	1.0
<i>Semele rubropicta</i> Dall, 1871	0.9
<i>Pugettia</i> sp.	0.8
<i>Diplodonta orbellus</i> (Gould, 1852)	0.8
<i>Humularia kennerlyi</i> (Reeve, 1863)	0.7
<i>Panopea generosa</i> (Gould, 1850)	0.6
<i>Telmessus cheiragonus</i> ¹ (Tilesius, 1815)	0.4
<i>Modiolus rectus</i> (Conrad, 1837)	0.3
<i>Pododesmus cepio</i> (Gray, 1850)	0.2
<i>Diodora aspera</i> (Rathke, 1833)	0.2
<i>Solen sicarius</i> (Gould, 1850)	0.1
<i>Crepidula</i> sp.	0.1
<i>Strongylocentrotus</i> ² sp.	0.03
<i>Lyonsia saxicola</i>	0.03
Other Items ³	0.14

¹Crustacea

²Echinodermata

³These included traces of limpets (Acmaeidae), unidentified crabs, and occasionally octopuses.

same area were feeding on different prey as indicated by shell collections from dens. For example, one octopus began to feed heavily on the bivalve *Diplodonta orbellus* (60% of the prey items at its den) but the same diet was not observed in other dens nearby. In one study site in Clayoquot Sound, octopuses fed mainly on *Clinocardium nuttallii*, *Cancer productus* and *Protothaca staminea* while 2 octopuses in that area were feeding heavily on the bivalve *Gari californica* (46% and 32% of 100 and 62 items, respectively). In these 2 cases the clam *G. californica* occurred frequently in the diet throughout the whole summer. The octopus making heaviest use of such clams also fed more on the clam *Saxidomus giganteus* (9%) than octopuses in nearby dens. In another study site in Clayo-

quot Sound, octopuses made considerable use of the commercially important Dungeness crab *Cancer magister*. For

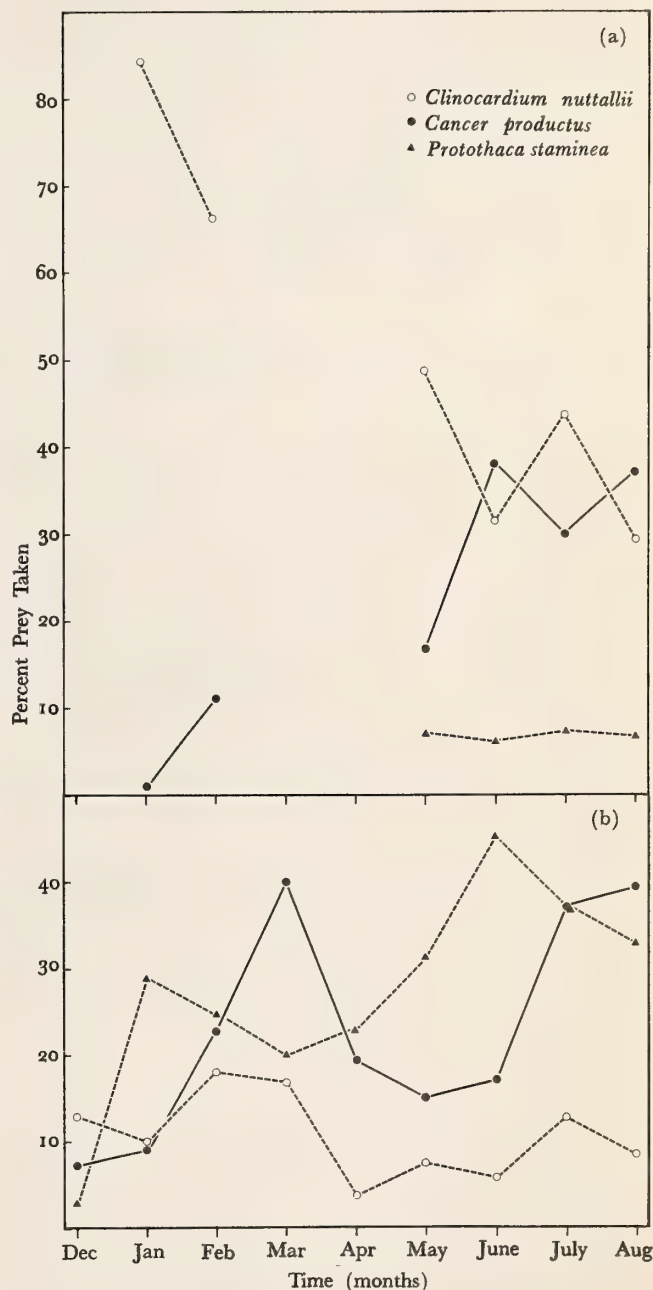


Figure 1

Variation in the percentage of selected prey in the diet of octopuses in Clayoquot (a) and Barkley Sounds (b) based on shells collected from den entrances

example, in 1 den, 27 of 100 prey items consisted of these crabs. Another den nearby however, showed heavy use (42%) of the rock crab (*C. productus*) over the same period.

The idea of individual differences in octopus feeding was also supported by a multiple regression analysis relating the percent crabs in the diet to den site, depth and time of year. Den site, presumed to represent an individual octopus, and time of year were significant factors ($p < 0.01$). However, the regression explained at most only 28% of the variation in crab use. Unfortunately no quantitative estimates of crab availability were made for the study sites so that this important variable was not included in the analysis.

FORAGING AREA AND FOOD SELECTION

Although octopuses were only rarely observed feeding, the items in the diet and the characteristics of the habitat provide some information on their foraging. The composition of the diet indicates that foraging occurs more often on soft bottoms than on rock surfaces. The absence of mussels (*Mytilus* spp.) in the diet, in spite of their abundance in the intertidal zone, may indicate an avoidance of either mussels themselves or the rocky intertidal habitat in which they are found. Most of the octopus dens in Clayoquot Sound were close to eel grass beds where cockles *Clinocardium nuttallii* were available in great abundance. Frequent foraging trips to such eel grass beds would explain the high percentage of these items in the diet. Octopuses making heavy use of *Protothaca staminea* had dens located near gravel beaches where these clams are found. Both *C. nuttallii* and *P. staminea* are found close to the surface of the sediments and are presumably easy to obtain by octopuses. Bivalves found deep in the sediment were utilized less. Thus, octopuses fed very little on geoducks (*Panopea generosa*) in spite of their great abundance in the area and their occurrence in a variety of types of bottoms.

There is evidence that octopuses do not feed upon some potential prey close to their dens. *Haliotis kamtschatkana* was not heavily preyed upon and in many cases this species was observed close to octopus dens, even at the entrance. Similarly, the rock scallop *Hinnites giganteus* was often present near dens but was ignored at least temporarily. In one den, seven of these were attached near the den opening.

Certainly, based on qualitative impressions, the low use of prey like *Hinnites giganteus*, *Haliotis kamtschatkana*

and *Panopea generosa* did not reflect a low abundance of these prey. In fact, since the time of the study, commercial harvesting of *P. generosa* has been initiated in the area because of its great abundance.

SIZE OF PREY

Collections of shells from dens indicated that prey size varied over a wide range. Sizes of the bivalve *Protothaca staminea* taken by octopuses varied from 15.5 mm. to 70 mm. The size distribution of eaten clams was unimodal with a peak in the 40-45 mm size class (Figure 2). The size distributions of these clams were similar in shell collections from both Barkley and Clayoquot Sounds. Sizes of abalone (*Haliotis kamtschatkana*), butter clams (*Saxidomus giganteus*) and crabs (*Cancer* spp.), all of commercial importance, taken as prey also varied over a wide range. For all 3 types of prey, the sizes taken most frequently were in the range 75-95 mm (Figure 2). The only information on sizes of these prey available in the habitat is from an abalone survey reported by QUAYLE (1971) in one of the octopus study sites. The survey was carried out in 1963 and indicated a mean length of 108 mm with a range of 66-137 mm. However, abalone have been commercially harvested along with red sea urchins *Strongylocentrotus franciscanus* (A. Agassiz, 1863) in the area since that time. No information is available on current size distribution.

Figure 3 shows that the mean size of all prey together increased with increasing size of octopus ($p < 0.05$). Similarly, size of *Clinocardium nuttallii* increased with size of octopus ($p < 0.05$) although the relationship was not significant for *Protothaca staminea*. In spite of the statistical significance, considerable variability was present in sizes taken by octopuses of different sizes. However, further support comes from current feeding experiments with a very small octopus which selects small prey from a variety of sizes available (S. Robinson, personal communication).

GROWTH RATES IN THE FIELD

Recaptures of tagged octopuses provided growth data under natural conditions. The weight changes for 15 tagged octopuses are given in Table 2. The gain in weight per day varied from 13.9 g to 109.4 g. When expressed as a fraction of the mean weight during the observation period, these gains indicated daily growth rates varying from 0.1 to 1.8 percent.

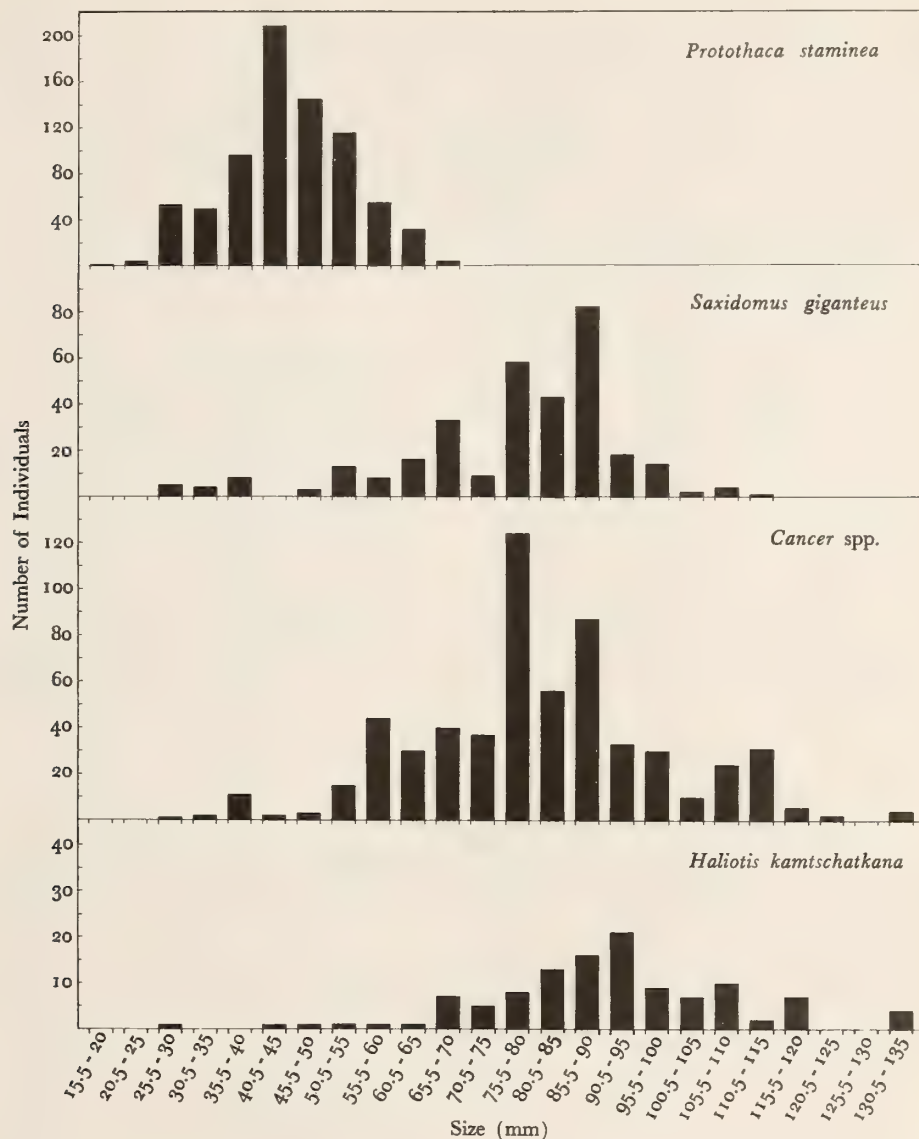


Figure 2

Size frequency histograms for commercially important prey species taken by octopuses

Average daily growth rates appeared to be relatively high in October (0.8-0.9), lower over the winter (0.1-0.6) and high again in spring and summer (0.5-1.8). This seasonal pattern is also evident when weights of individuals recaptured several times are examined (Table 3).

GROWTH RATES AND FEEDING OF CAPTIVE OCTOPUSES

The 2 octopuses in the large tanks in summer 1977 showed similar exploratory behaviour and prey manipulation

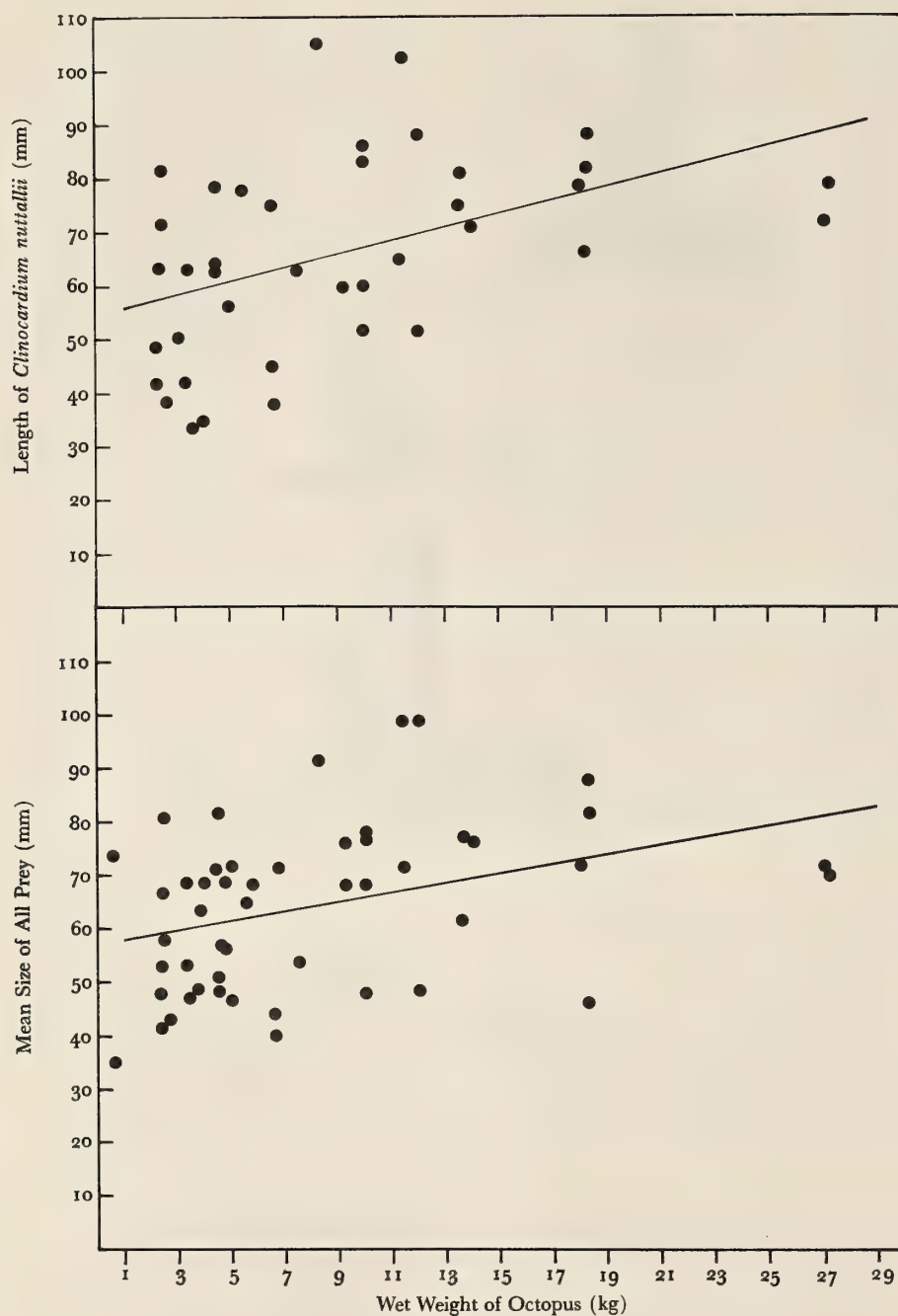


Figure 3

The relationship between size of octopus and size of prey based on wet weights of octopuses and length or maximum diameter of prey. The line was fitted by standard regression techniques

Table 2

Growth rates of tagged octopuses recaptured in Clayoquot Sound.
Octopuses 1-4 and 12 were tagged in 1978, all others in 1979.

Octopus	Sex	Observation period in days	Initial weight (kg)	Final weight (kg)	Gain in weight/day (g)	Average daily growth rate (%)
1	F	16 (Oct.)	9.5	10.8	78.1	0.8
2	F	16 (Oct.)	12.0	13.8	109.4	0.9
3	F	118 (Oct.-Feb.)	10.5	18.4	66.9	0.5
4	M	82 (Oct.-Jan.)	10.3	17.4	86.6	0.6
5	M	36 (Jan.-Feb.)	15.7	16.7	27.8	0.2
6	F	36 (Jan.-Feb.)	16.4	17.4	27.8	0.2
7	F	36 (Jan.-Feb.)	17.9	20.2	63.9	0.3
8	F	109 (Jan.-April)	11.4	16.3	44.9	0.3
9	F	36 (Jan.-Feb.)	10.7	11.2	13.9	0.1
10	F	73 (Feb.-April)	11.2	13.7	33.6	0.3
11	F	67 (April-June)	8.9	13.6	70.2	0.6
12	F	210 (Oct.-May)	6.3	13.3	33.3	0.3
13	F	12 (July)	7.5	8.8	108.3	1.3
14	M	14 (July-Aug.)	2.9	3.8	60.7	1.8
15	F	25 (July-Aug.)	13.4	15.3	74.0	0.5

Table 3

Growth of tagged octopuses recaptured at different times of the year.

Octopus (from table 2)	Sex	Observation period in days	Initial weight (kg)	Final weight (kg)	Gain in weight/day (g)	Average daily growth rate (%)
3	F	16 (Oct.)	10.5	12.9	150.0	1.3
		66 (Oct.-Jan.)	12.9	17.2	65.2	0.4
		36 (Jan.-Feb.)	17.2	18.4	33.3	0.2
8	F	36 (Jan.-Feb.)	11.4	12.2	22.2	0.2
		73 (Feb.-April)	12.2	16.3	56.2	0.4
11	F	35 (April-May)	8.9	11.3	67.1	0.7
		32 (May-June)	11.3	13.6	73.4	0.6

when freshly caught bivalves were placed in the aquaria. Shells were momentarily grasped and then either dropped or held; all were usually touched even if they were not eaten. Often several bivalves were gathered under the webbing at the same time and carried to either an artificial den or a 'preferred' corner. At times the bivalves

were eaten where they were found. Approximately 30% of the shell debris was scattered in other parts of the tanks, the rest being at the den.

The following bivalves were presented to captive octopuses in various combinations: *Tresus capax*, *Siliqua patula* (Dixon, 1789), *Humularia kennealyi*, *Mytilus cali-*

forianus Conrad, 1837, *Mya arenaria* Linnaeus, 1758, *Protothaca staminea*, and *Saxidomus giganteus*. All of these bivalve species were fed on at least once by the captive octopuses even though *Mytilus californianus* and *Mya arenaria* did not show up in shell collections from natural dens. When all were presented at once to an octopus, the soft shelled clam (*M. arenaria*) and the gaper clam (*Tresus capax*) were eaten before both *P. staminea* and *S. giganteus*. This occurred even though all were first examined by the octopus, and in spite of the fact that the latter two are most frequent in the diet of wild octopuses. This apparent preference occurred in 5 separate experiments. In one case, a captive octopus attacked and consumed both a *M. arenaria* (length 8.8 cm) and a *T. capax* (length 11.3 cm) in 2 hours. The shell of *M. arenaria* was cracked open, while that of the *T. capax* appeared to simply have been pried apart with no effect on the shell. Drill holes were commonly observed in shells of *P. staminea* fed on by the captive octopuses.

In the studies carried out in the fall of 1978, octopuses held in boxes suspended in the inlet were fed *ad libitum* with fish (*Merluccias productus*), crabs (*Pugettia producta*), abalone (*Haliotis kamtschatkana*) and bivalves (*Protothaca staminea* and *Mya arenaria*). In almost all cases the fish was eaten first, then crabs, followed by the soft shelled clam *M. arenaria* and finally the other prey items. Prey handling was observed through the plexiglas bottom of the holding box. When handling the crabs (*P. producta*) the octopus first attempted to pull the carapace off. If this failed, the octopus would turn the crab ventral side up and drill the abdomen of the crab (9 out of 15 cases). Female crabs were drilled more often than males (77%, n = 18; 33%, n = 12). Handling of *M. arenaria*

was similar to that observed in the experiments in summer 1977. *M. arenaria* was pulled apart or cracked open while *P. staminea* was drilled.

All captive octopuses grew over the fall 1978 observation period, including those in the box in the inlet as well as those in the aquaria. Average daily growth rates varied from 0.6% to 1.1% (Table 4). The average conversion ratio was 1.7:1.

Since growth was frequently measured it was possible to detect variation in food intake with changing composition of available prey. In all cases octopuses ate more food relative to their body weight when fish and crabs were available than when only crabs were available. For example, octopus number 3 (Table 4) consumed 1.3% of its body weight per day when fish and crabs were available, and only 0.95% when crabs alone were present.

DISCUSSION

Models of optimal foraging for refuging predators have indicated that such predators will adopt search patterns that locate feeding patches some distance away from the refuge rather than ones nearby (MORRISON, 1978). According to Morrison, such tactics might explain why natural predators seem to ignore nearby prey, and why foraging ranges of some animals can be so broadly overlapping. *Octopus dofleini* is a refuging predator leaving its den usually at night (personal observations) to go on foraging trips, and often ignoring potential prey items near the den itself. The appearance of considerable numbers of *Protothaca staminea* in the diet suggests that *O. dofleini* may make continuing use of particular feeding sites since

Table 4

Growth and food intake of 6 captive octopuses.
The first 4 octopuses were kept in the laboratory while 5 and 6 were in boxes submerged in an inlet.

Octopus	Observation period (days)	Initial weight (kg)	Gain in weight/day (g)	Average daily growth rate (%)	Daily feeding rate (%)	Daily feeding rate (g/day)	Food conversion (%)	Food conversion (ratio)
1	60	2.8	22.5	0.7	1.2	(39.5)	39.6	(2.5:1)
2	60	2.8	41.7	1.0	1.2	(53.6)	74.7	(1.3:1)
3	40	2.5	33.8	1.1	1.4	(45.9)	73.6	(1.4:1)
4	40	2.8	37.5	1.1	1.2	(43.2)	87.0	(1.2:1)
5	45	4.0	44.4	0.9	2.0	(100.4)	44.3	(2.3:1)
6	42	3.3	21.4	0.6	1.3	(48.6)	44.1	(2.3:1)

this clam occurs in discrete intertidal gravel beds some distance from the dens. Thus, *O. dofleini* acts like many predators faced with patchy prey distributions and a refuging mode of life (MORRISON, 1978).

The observation that several clams were picked up at one time by captive octopuses makes energetic sense and agrees with the observations of YARNALL (1969) who reported that *Octopus cyaneus* transported several crabs at one time. The wide variety of prey items in the diet of *O. dofleini* suggests that it is an opportunistic feeder. Nevertheless, the items occurring most frequently in the diet are those that are numerous and readily accessible like *Clinocardium nuttallii* and *Protothaca staminea* which occur in dense populations close to the surface of the sediments. Considerable feeding on *P. staminea* has also been reported for *O. bimaculatus* by FOTHERINGHAM (1974), who suggested that octopuses might act as keystone predators in the same manner as *Pisaster ochraceus* (Brandt, 1835) in *Mytilus* beds (PAINE, 1966). However, at the present time there are no data to support his contention. As in the present study, Fotheringham also found little or no use of the mussel *Mytilus* spp. by octopuses in spite of the abundance of this potential prey item. Nevertheless, captive *O. dofleini* will feed readily on these and other items uncommon in their natural diet, especially if they are easy to break open and feed upon. HARTWICK *et al.* (1968c) showed that prey handling by *O. dofleini* involved breaking apart shells, pulling them apart, or drilling and, in this regard, these octopuses were similar to other species (PILSON & TAYLOR, 1961; ARNOLD & ARNOLD, 1969; WODINSKY, 1969). The apparent preferential selection of particular food items, like *Mya arenaria* which does not require drilling, over other bivalves and the individual variation in diet shown in the field presumably reflect the learning capabilities of these organisms (WELLS, 1978).

Although fish remains were usually not found at den sites, they may be taken as prey. Their absence from den collections may indicate that scavengers quickly remove any remains or that they are fed on away from the den. Observations in the laboratory indicated that most prey were taken to the den, although up to 30% may be scattered some distance away. During the present study one octopus was observed feeding on a crab in the open away from any den sites, and occasionally small areas have been found with an accumulation of shells possibly indicating feeding by an octopus. Thus, shell collections at dens may provide an incomplete picture of the diet of octopuses. Long foraging trips by octopuses and the existence of resting and feeding sites away from dens have been noted in other studies (YARNALL, 1969; HOCHBERG & COUCH, 1971).

Although the relationship between prey size and size of octopus is admittedly weak, current studies with small individuals provide support for the idea. The relationship may only apply to prey items like cockles, *Clinocardium nuttallii*, which are typically broken apart rather than drilled. Larger cockles are presumably more difficult to handle and are fed on more frequently by larger octopuses. However, it may be that over the range of sizes considered in the present study, there is no real size effect and certainly, further work on the matter is called for.

Both food intake and growth of octopuses are affected by temperature (MANGOLD & BOLETZKY, 1973). In the cold waters off Vancouver Island (7.5°C-15°C surface temperature), *Octopus dofleini* showed growth rates comparable to those reported for *O. vulgaris* kept in constant temperatures of 10°C (MANGOLD & BOLETZKY, 1973). Daily growth rate of *O. vulgaris* at 10°C varied from 0.35 to 1.57% while that of tagged *O. dofleini* in the present study ranged from 0.1 to 1.8%.

Growth rates in both field and laboratory conditions in the present study were comparable, although only one octopus in the tagged population was as small as those in the laboratory and its growth rate was in fact higher (1.8% compared to 1.1% or less). The possible sources of differences in growth in laboratory octopuses compared with free living octopuses have been discussed by JOLL (1977).

A careful examination of Table 2 indicates that growth rates and food intakes are lower for larger octopuses when comparisons are made at the same time of year. This agrees with data presented for *Octopus cyaneus* by VAN HEUKELEM (1973). The data on tagged *O. dofleini* indicate that an octopus weighing between 6 and 11 kg. may double its weight in just over a 5 month period. Since sizes of octopuses in the field study were not comparable to those in the laboratory, it is not clear whether the field rates were maximal or whether food was limiting. The high average daily growth rate of one small octopus in the field suggests that at least in that study area food is plentiful. Although JOLL (1977) suggests that it is unlikely that octopuses in the field live in a condition of excess food supply, WELLS (1978) refers to data from experiments which indicate that food availability is probably not a limiting factor. The present results appear to confirm this.

JOLL (1977) suggests that daily feeding rates of *Octopus tetricus* need to be 2% or more to satisfy their maintenance requirements, and that gross growth efficiencies under those conditions range from 11 to 76% (9.1:1 to 1.3:1) with a mean of 46.8% (2.1:1). VAN HEUKELEM (1976) estimates the gross growth efficiency for *O. cyaneus* and *O. maya* to be 38.3% and 39.5%, respectively, but suggests that on a caloric basis these figures may be as high as 60%.

In the present study gross growth efficiencies ranged from 39.6 to 87% (2.5:1 to 1.2:1) with daily growth rates from 0.6 to 1.1%. The range in gross growth efficiency is similar to that reported for *O. vulgaris* by MANGOLD & BOLETZKY (1973).

Although growth data are lacking for the planktonic juveniles, nevertheless, the present study does permit some speculation on the possible lifespan of *Octopus dofleini*. The growth information recorded during the present study covers the range from 2.5 to 20.2 kg. By placing weight changes in consecutive order an estimate of time for growth over the total range is obtained. This comes to 470 days. Depending on the growth rate at early stages *O. dofleini* may take between 2 and 3 years to reach maximum size. This estimate may be modified after current tagging and growth studies are completed.

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Observations on the Embryonic Development and Early Post-Embryonic Behavior of *Octopus bimaculatus*

(Mollusca : Cephalopoda)

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(4 Text figures)

INTRODUCTION

Much of the classical cephalopod development research has concerned decapods (see ARNOLD, 1971; ARNOLD & WILLIAMS-ARNOLD, 1977). The first thorough description of octopus development was given by NAEF (1928). At present, development of octopuses has been studied in only a few species. The development of *Octopus vulgaris* (NAEF, 1928; BOLETZKY, 1971), *O. tetricus* (JOLL, 1976; 1978), and *Eledone cirrosa* (MANGOLD, BOLETZKY & FROSCH, 1971; FUCHS, 1973a; 1973b) has been described in detail. Developmental observations have also been made for *Eledone moschata* (BOLETZKY, 1974), *Hapalochlaena maculosa* (DEW, 1959; TRANTER & AUGUSTINE, 1973), *H. lunulata* (OVERATH & BOLETZKY, 1974), *O. joubini* (BOLETZKY, 1969; BOLETZKY & BOLETZKY, 1969; OPRESKO & THOMAS, 1975), *O. briareus* (BOLETZKY, 1969), *O. cyanea* (DEW, 1959), and *O. dofleini* (GABE, 1975).

Octopus bimaculatus Verrill, 1883 is a common member of the intertidal and subtidal communities of southern California. Female octopuses lay strands of eggs in protected rock shelters and care for the eggs until they hatch. The young are planktonic for 2-3 months (Hochberg, personal communication) before settling to the bottom to assume a benthic existence. This paper describes some of the major aspects of the embryonic development and early post-embryonic behavior of *O. bimaculatus*.

MATERIALS AND METHODS

Research was conducted at the Catalina Marine Science Center on Santa Catalina Island (33°27'N; 118°29'W), 30 km S of Los Angeles, California USA. Between May

1976 and August 1979, 75 brooding octopuses were observed in the field. Regular collections of egg strands from two of these octopuses were used to identify the general course of *Octopus bimaculatus* development. Specific stages of development were investigated by supplemental collections of eggs from other octopuses. After observations and measurements, eggs were preserved in 95% ethanol. In 1978, brooding octopuses were censused approximately weekly to monitor development and determine total length of development (time from first egg laying to first hatching). Because octopuses could not be checked daily, development times are only estimates.

Several octopuses brooded eggs in the laboratory; regular collections were made from one of these. Egg strands from field collections were maintained in the laboratory in containers with a rapid, direct flow of seawater from beneath the eggs. Development proceeded normally in these egg strands for only a few weeks, after which the embryos were no longer viable. Only embryos collected during late stages of development could be maintained until hatching.

The temperature during development was determined by averaging temperature data (recorded at roughly weekly intervals) for the development period. Temperatures in 1977 through 1979 were recorded at the locations where octopuses were brooding. Field water temperatures for 1976 broods (N = 3) were recorded at brooding depth in a similar habitat 1 km away. Since all eggs (laboratory and field) developed at ambient sea temperatures, they were sometimes exposed to short-term temperature fluctuations of several degrees. In addition, all broods were subjected to seasonal warming trends in water temperature, so that temperatures at the end of embryonic development were higher than at the beginning. The effect of

The relationship between temperature and development time in *Octopus bimaculatus*. Development time is the number of days between first laying and first hatching of the eggs, and is plotted on a logarithmic scale; temperature is an estimate of the mean temperature during development. The equation for the line in $DT = -0.13(T) + 6.42$; $N = 17$; $r = -0.83$, $p < 0.01$

latus. Representative stages of development are illustrated in Figure 2.

After fertilization, blastodisc development takes place at the free end of the chorion (Stage 1 of Naef). From late stage I to stage VII, the yolk epithelium spreads away from the blastodisc towards the vegetal pole to form a yolk envelope (Figure 2a).

ROTATION AND REVERSAL

The embryos reverse their position in the chorion two times during development. The first reversal occurs at stage VII. Ciliary movement causes rotation of the embryo in a clockwise direction (as viewed from the micropyle, or free, end of the chorion), beginning about stage VIII. The embryo rotates at a rate of 1 rotation/10 minutes at stage X and 16° C. A second reversal at stage XIX returns the *Octopus bimaculatus* embryo to its original orientation within the chorion.

YOLK SACS AND CIRCULATORY SYSTEM

By stage IX, the yolk mass is divided into inner and outer yolk sacs. Pulsation of the outer yolk sac begins at this time and continues through stage XV. The size of the inner yolk sac decreases until stage XV. The inner yolk sac is distinctly bilobed, particularly as it becomes smaller (Figure 2e). At stage XV the inner yolk sac begins increasing in size, and continues to increase until hatching. During this period the size of the outer yolk sac decreases due to transfer of yolk from the outer to inner yolk sacs.

Regular heart beats occur by stage XV. Heart rate increases with advancing development. At 16° C, *Octopus bimaculatus* heart rate increased from 17 beats/min at stage XVIII, to 80 beats/min at stage XIX (stage XIX at 17° C).

ARMS AND SUCKERS

Arm buds first appear at stage IX; the arms are well developed by stage XII (Figure 2c). Three uniserial suckers appear simultaneously at stage XII; a fourth small sucker develops at the tip of the arms by stage XX. Arm movement is frequent at stage XVII, and by stage XVIII the arms move independently of each other and of body movement. At stage XX, the arms may be displaced to one side or near the head rather than neatly encircling the outer yolk sac.

PIGMENTATION

Pigmentation first develops at stage IX, when faint red retinal pigments appear. These pigments darken from tan at stage X to black by stage XIV. Ventral mantle chromatophores develop in the mantle integument at stage XV (Figure 2f; Table 1). Chromatophores on the dorsal surface, which appear in the inner integument closely surrounding the visceral mass, do not develop until stage XVII (Figure 2g). The number of mantle chromatophores, both dorsal and ventral, increases as development proceeds. At late stage XX, many small red chromatophores develop in the outer integument over the dorsal mantle and head.

Head chromatophores develop at stage XVII. Most dorsal head chromatophores develop simultaneously, although 3 additional chromatophores appear around each eye at stage XIX.

Arm chromatophores appear first on the ventral arms, at stage XVII, with chromatophores on the dorsal arms appearing at stage XVIII. Ventral arms have more chromatophores than dorsal arms through most stages, al-

Table 1

Sequence of chromatophore development in *Octopus bimaculatus*

Stage	Body		Head		Arms (per arm)		Funnel
	Ventral	Dorsal	Ventral	Dorsal	Ventral	Dorsal	
XV	10						
XVI	25						
XVII	25	10	2	10-12	2-3		
XVIII	35-40	20	2-4	10-12	3	2 (late)	2 (late)
XIX	40	25	2-4	16-18	4	2-3	4
XX	40-45	25	4-8	16-18	8	8	8

though by late stage XX arm chromatophore distribution is usually more equal.

A pair of funnel chromatophores appear at stage XVIII; by late stage XX there are 8 funnel chromatophores.

There is some individual variation in chromatophore number. Location of chromatophores is also variable; for instance, ventral mantle chromatophores may be neatly aligned in rows in some individuals and randomly scattered over the mantle surface in others.

HATCHING

Octopus juveniles from the same brood hatched over a period of several days. In the laboratory, animals were observed pumping energetically in their egg cases prior to hatching. The egg case usually split near its free end, and the juveniles quickly emerged mantle-first. Agitation of the eggs promoted hatching in both the laboratory and the field. Juveniles which hatch in the field do not have an external yolk sac. Juveniles which were partially raised in the laboratory hatched prematurely. Premature hatching of a given individual was normally completed in 3 to 6 minutes. The external (=outer) yolk sac of premature juveniles occasionally became stuck inside the egg case. In addition to normal mantle contractions and pumping, these juveniles would intermittently lift their bodies up slowly and then drop down, apparently trying to pull loose or "shimmy" out of the egg case. Stuck juveniles would attempt to free themselves for up to 30 minutes, but usually died.

JUVENILE CHARACTERISTICS

Average total length of newly hatched juveniles was 4 mm, with a dorsal mantle length of 2.6 mm and width of 1.5 mm. Arm length was 40% of the mantle length. There were 4 suckers per arm. The newly hatched juvenile chromatophore pattern is shown in Figure 3. The large dorsal body chromatophores lie underneath the mantle and surround the visceral mass; the ventral body chromatophores lie just under the skin covering the mantle.

Within three days after hatching, a few more chromatophores develop, primarily around the eyes and on the web between the arms. Dorsal and ventral head and body chromatophores remain the same as early post-hatching. There are 6-7 suckers per arm, but the suckers near the tips of the arms are not well developed. The weight of 6-day old unfed juveniles was about 1.5-2.0 mg.

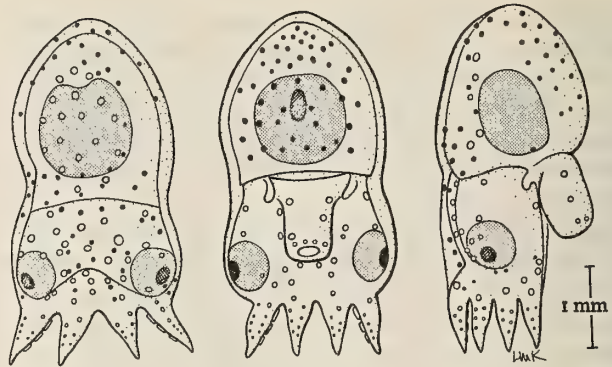


Figure 3

Distribution of chromatophores on newly hatched *Octopus bimaculatus*

POST-HATCHING BEHAVIOR

Newly hatched juveniles of *O. bimaculatus* were planktonic. The juveniles swam both forward (arms-first) and backward (mantle-first), but usually swam backward. Average speed in an observation dish (20 mm diameter), was 1 mm/sec, with frequent bursts of 5 mm/sec. In a 30 cm diameter by 45 cm deep container, juveniles swam somewhat faster but followed the same swimming pattern: slow, regular swimming most of the time, interspersed with rapid bursts of speed covering several centimeters. Juveniles usually swam with chromatophores expanded, but frequently the chromatophores were momentarily contracted. The arms were moved to some extent while swimming.

Although many juveniles swam throughout the entire depth of the container, the majority swam near the bottom, around the edge of the opaque white container; these juveniles repeatedly swam into the wall of the container, rebounded and swam into the wall again. Juveniles accumulated at the lighted region of an otherwise darkened container; they appeared to locate the lighted area by haphazard movements, but remained in the area once it was encountered. When the lighted region was moved, the aggregation of larvae gradually dispersed, then reformed at the newly lighted area.

The swimming behavior of several juveniles which hatched in the field was also observed. All juveniles consistently swam upwards, with their mantles oriented either vertically or at approximately 45°. They did not necessarily swim with the current, even though it was very

strong. Two juveniles were observed for several minutes. The first swam to within 1-2 m of the surface, and was still swimming upwards when observations were terminated. The second juvenile also swam upwards, but nonetheless barely managed to stay at the same depth (5 m below the surface).

Inking was not observed in the laboratory until the juveniles were 4 days old, and even then it only occurred in response to being disturbed. Younger juveniles did not ink, even when handled.

After the contents of a plankton tow were added to the container holding the octopus juveniles, juveniles were occasionally observed to settle on the bottom and nearly double over, reaching under their body with their arms. The function of this behavior is unknown, but it may have been an attempt to remove debris introduced with the tow contents. Several octopuses were observed to attach themselves firmly to the bottom with all arms; one individual moved 1-2 mm along the bottom in this manner, with mantle perpendicular to substrate and arms extended. Small (< 10 mm dorsal mantle length) *Octopus bimaculatus* in the field occasionally exhibit this behavior while confined in a diver's hand.

Three-day old juveniles fed on both laboratory-hatched brine shrimp and natural plankton. One capture was observed: the octopus followed the prey item (probably a calanoid copepod) for several centimeters, swimming arms first, then rushed forward and captured it with its arms. Although a number of juveniles initially fed readily, as evidenced by full guts, later efforts to feed them were unsuccessful.

Four days after hatching in the laboratory, most octopuses were still alive, but were inactive and swam only when disturbed. Most octopuses were dead six days after hatching. The inner yolk sac was noticeably reduced three days after hatching, and completely depleted after six days, so the juveniles probably died of starvation.

DISCUSSION

In 1923, Naef proposed that octopus species with large eggs be included in a separate genus, *Paraoctopus*. PICKFORD & McCONNAUGHEY (1949), working with *Octopus bimaculatus* and *O. bimaculoides*, showed that separate generic status for species with large eggs was not warranted. Rather than simply representing a phylogenetic characteristic, octopus egg size relative to adult size is clearly correlated with mode of juvenile life (BOLETZKY, 1974): octopuses with relatively small eggs have planktonic young, while octopuses with relatively large eggs

have benthic young. *Octopus bimaculatus* egg size is approximately 5% of the average adult dorsal mantle length. As expected on the basis of relative egg size, newly-hatched *O. bimaculatus* juveniles are planktonic. The relative egg size of *O. bimaculatus* is essentially identical to that of *O. rubescens*, *O. salutii*, *O. vulgaris*, and *Eledone cirrosa* (Hochberg, personal communication; OVERATH & BOLETZKY, 1974), and probably to many other species with planktonic young.

The development time of *Octopus bimaculatus* eggs is inversely correlated with water temperature. To explore the generality of the temperature/development time relationship found in *O. bimaculatus*, I have compared information in the literature for other octopus species. Because insufficient data exist at present to evaluate the influence of egg size on development time (although BATHAM, 1957 and MANGOLD *et al.*, 1971 assert its importance), only octopus species with planktonic juveniles (*i.e.*, relatively small eggs) are included. Three species besides *O. bimaculatus* have been studied sufficiently to enable comparison.

The development time of each of the four species is inversely correlated with mean water temperature (Figure 4; *Octopus bimaculatus*: $N=17$, $r=-0.83$, $p < 0.01$; *O. vulgaris*: $N=30$, $r=-0.87$, $p < 0.01$; *O. cyanea*: $N=11$, $r=-0.78$, $p < 0.01$; *O. tetricus*: $N=7$, $r=-0.87$, $p < 0.01$). There is considerable variability in development time within each species, up to 20 days at the same temperature; over a short temperature range this variation could mask an overall trend. Nonetheless, the significant and consistent trend over a total range of 17°C suggests that this relationship is generally true. Although the \ln development time/temperature relationship appears essentially linear, at temperature extremes there are marked non-linearities. The decelerating rate of development at low temperatures suggests the presence of a minimum temperature below which development will not take place.

The inverse correlation between development time and water temperature has previously been suggested for *O. vulgaris* by MANGOLD-WIRZ (1963) and MANGOLD & BOLETZKY (1973). The analysis presented here corroborates the existence of such a relationship in *O. vulgaris* and suggests that it exists for octopuses in general. OPRESKO & THOMAS (1975) state that there is no apparent correlation between temperature and development time in *O. joubini*. However, analysis of the relationship between average temperature and development time (data from table 2 of OPRESKO & THOMAS) indicates that, in spite of a temperature range of only 1.9°C, there is a significant negative correlation ($N=10$, $r=-0.64$, $p < 0.05$).

Some species-specific differences in development time are expected as a result of differences in the length of time

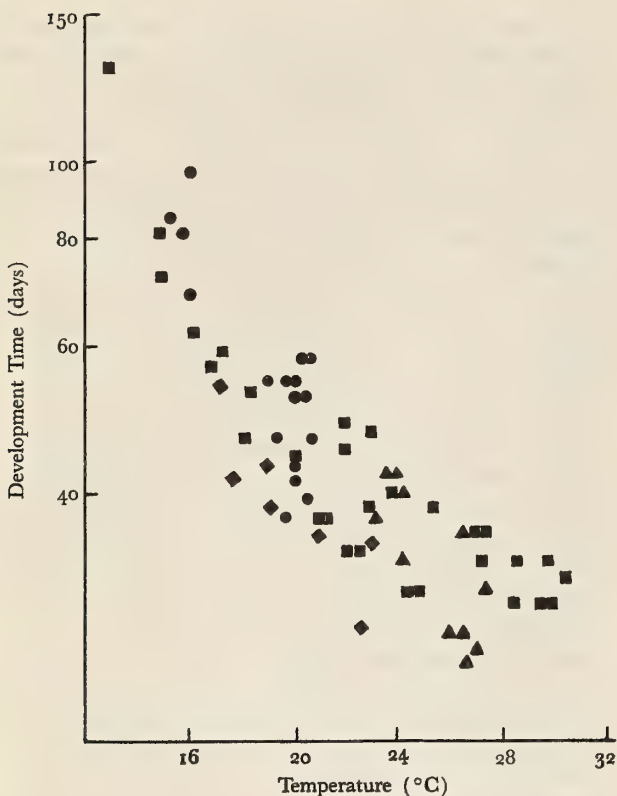


Figure 4

The relationship between temperature and development time in octopuses with planktonic young. Development time is plotted on a logarithmic scale

- - *Octopus bimaculatus* (this paper)
- - *Octopus vulgaris* (MANGOLD-WIRZ, 1963; WODINSKY, 1972; MANGOLD & BOLETZKY, 1973)
- ▲ - *Octopus cyanea* (VAN HEUKELEM, 1973)
- ◆ - *Octopus tetricus* (JOLL, 1976; 1978)

spent in the plankton, environment inhabited, etc. Differences between species would also be expected if the amount of yolk (*i.e.*, egg size) were more important than temperature in determining development time (MANGOLD *et al.*, 1971). The data for the four species examined in Figure 4 appear to fit a single \ln development time/temperature relationship. (The equation for that line is $\ln DT = -0.07 (T) + 5.21$; $N = 65$, $r = 0.84$, $p < 0.01$.) Small sample sizes, large intraspecific variability, and dissimilar investigative techniques make comparisons between species imprecise. However, examining the differences between *Octopus bimaculatus* and *O. tetricus* shows that in spite of a larger egg size (3.8 mm for *O. bimacu-*

latus, 2.4 mm for *O. tetricus*) several clutches of *O. bimaculatus* developed very close to the mean development time and temperature for *O. tetricus*. There may be no actual differences between the 4 species, or perhaps differences are slight because all have relatively small eggs. In any case, there is not enough information to distinguish species-specific differences at this time, and future work here is clearly indicated.

The inverse correlation between development time and temperature may explain in part the seasonal migrations into shallow water for breeding which have been reported for a number of octopus species (*O. vulgaris*, MANGOLD-WIRZ, 1963; *O. defilippi*, VÉRANY, 1851; MARCHAND, 1907; *O. dofleini*, MOTTET, 1975; *O. rubescens*, Hochberg, personal communication). Since shallow water is almost invariably warmer than deep water, migration to shallow water to breed will reduce development time. Shorter development time could reduce mortality by exposing the brooding female and her eggs to predators for a shorter period of time.

The embryonic development of *Octopus bimaculatus* closely resembles that of *O. vulgaris* (NAEF, 1928) and *O. tetricus* (JOLL, 1978). The development pattern of major embryonic features is nearly identical for the 3 species, with differences resulting primarily from small shifts in timing. For example, *O. bimaculatus* undergoes its second reversal at stage XIX, rather than stage XVII as in *O. vulgaris* and *O. tetricus*.

The most notable difference in development among these 3 species occurs in pigmentation. FIORONI (1965) has documented chromatophore development in *O. vulgaris* in detail, thus allowing comparison with *O. bimaculatus*. In *O. vulgaris*, ventral body chromatophore number increases rapidly to 15 chromatophores at stage XVI, then gradually increases to 20 chromatophores at stage XX. In contrast, *O. bimaculatus* ventral body chromatophore number increases very rapidly to about 40 chromatophores at stage XVIII and stops. Dorsal body chromatophores appear later in *O. bimaculatus* and increase to a greater number. Finally, dorsal head chromatophore development is nearly simultaneous in *O. bimaculatus*, rather than sequential as in *O. tetricus* (JOLL, 1978) and *O. vulgaris*.

A comparison of morphometrics of newly hatched juveniles for 9 species of octopods with planktonic juveniles (Table 2) reveals a wide range of sizes, from 2.5 mm to 7.0 mm in total length. There is also considerable variation in the number of suckers per arm (3 to 14), which may be inversely correlated with the length of time the juveniles spend in the plankton, since benthic juveniles hatch with many more suckers per arm (*O. joubini*, 26, and *O.*

Table 2

Morphometrics of newly hatched planktonic juveniles

Species	Total length (mm)	Mantle length (mm)	Mantle length (% adult ML)	Arm length (% ML)	Number of suckers per arm	Reference
<i>O. tetricus</i>	2.5	1.5 ¹	—	50 ¹	3	JOLL, 1976, 1978
<i>O. vulgaris</i>	3.0	2.0	2	35	3	BOLETZKY, 1969, 1977; OPRESKO & THOMAS, 1975
<i>H. lunulata</i>	—	2.3	4	50	10	OVERATH & BOLETZKY, 1974
<i>R. australis</i>	3.7	2.4 ¹	—	43	4	BROUGH, 1965
<i>O. bimaculatus</i>	4.0	2.6	5	40	4	This paper
<i>O. dofleini</i>	—	3.5	—	50	11-14	GABE, 1975
<i>O. salutii</i>	—	3.5	3.5	—	4	BOLETZKY, 1977
<i>O. maorum</i>	7.0	4.5 ¹	—	50 ¹	7-8	BATHAM, 1957
<i>E. cirrosa</i>	—	4.5	3.5	50	8	MANGOLD <i>et al.</i> , 1971

¹measured from figure

briareus, 35, MANGOLD *et al.*, 1971; *H. maculosa*, 20, OVERATH & BOLETZKY, 1974). The similarity in relative arm length, pointed out previously by OVERATH & BOLETZKY (1974), may also be related to a planktonic existence, since benthic juveniles have relatively longer arms (100-160% of dorsal mantle length, MANGOLD *et al.*, 1971; OVERATH & BOLETZKY, 1974). The presence of long arms at hatching may be an adaptation to an immediately benthic mode of life; while the arms and suckers of planktonic juveniles are suitable for holding onto floating objects (JOLL, 1978), they would not be adequate for extensive crawling on the bottom (BOLETZKY, 1977). In *O. bimaculatus* juveniles, attachment to the bottom seemed to be a response to disturbance, and the short movement of one juvenile was definitely not normal crawling behavior.

The distribution of chromatophores on newly hatched juveniles varies considerably from species to species. Chromatophore patterns present at hatching are generally related to the habit of the newly hatched young (WELLS & WELLS, 1977). For instance, *Octopus briareus* young, which are benthic, hatch with a well developed and dense assemblage of chromatophores (WOLTERDING, 1971), while *O. bimaculatus* juveniles hatch with fewer chromatophores. BOLETZKY (1977) suggests that the number of chromatophores is merely related to body size rather than post hatching mode of life. However, a comparison of species with newly hatched octopuses of the same size, such as *Hapalochlaena maculosa* (figure 7 of TRANTER & AUGUSTINE, 1973) and *O. maorum* (figures 1 and 2 of BATHAM, 1957), indicates that the planktonic juveniles have fewer chromatophores.

There are also distinct if less dramatic differences in chromatophore patterns among species with planktonic

young. *Octopus bimaculatus* has fewer dorsal body and arm chromatophores than *O. maorum* (BATHAM, 1957) but more than *O. tetricus* (JOLL, 1976) and *O. vulgaris* (FIORONI, 1965), as might be expected on the basis of size (Table 2). However, in spite of its intermediate size *O. bimaculatus* has a great many more ventral mantle chromatophores than *O. tetricus*, *O. vulgaris* or *O. maorum*. Presumably, the dissimilar chromatophore patterns have an adaptive value, perhaps relating to dissimilar conditions in the plankton experienced by the various species.

The continuous upward swimming of *Octopus bimaculatus* juveniles immediately after hatching in the field is consistent with the positive phototaxis exhibited in the laboratory. This behavior, which apparently has not been reported for other octopus species, would ensure that the young maintain an appropriate position in the water column while planktonic.

SUMMARY

The development time of *Octopus bimaculatus* is inversely correlated with water temperature. Comparison with data for 3 other species of *Octopus* with planktonic young indicates that the development times of all 4 species exhibit a similar response to temperature.

The embryonic development of *Octopus bimaculatus* closely resembles that of other octopus species with planktonic young. The development patterns of major embryonic features are nearly identical to that of *O. vulgaris* and *O. tetricus*, with differences resulting primarily from small shifts in timing. The most noticeable differences in development occur with respect to pigmentation, in both num-

ber of chromatophores and the sequence of their development.

Octopus bimaculatus juveniles from the same brood hatched over a period of several days. The newly hatched young were planktonic. The typical juvenile swimming pattern in the laboratory involved slow, regular swimming interspersed with rapid bursts of speed covering several centimeters, although juveniles in the field seemed to swim at a constant speed. In the laboratory, juveniles exhibited positive phototaxis. Some 3-day old juveniles fed on brine shrimp and natural plankton. Nevertheless, most laboratory-reared juveniles were dead 6 days after hatching, probably from starvation.

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Reproductive Biology of a Population of *Perumytilus purpuratus* at El Tabo, Chile

(Mollusca : Bivalvia : Mytilidae)

BY

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(2 Plates; 3 Text figures)

INTRODUCTION

Perumytilus purpuratus (LAMARCK, 1819), quite abundant in the intertidal zone, has been found in the Pacific Ocean from Ecuador to the Strait of Magellan and in the Atlantic as far as Santa Cruz, Argentina (OSORIO & BAHAMONDE, 1968); it was obtained also from the Quaternary of Cahuil in Chile and from the Araucanian and Pampean in Argentina (CARCELLES, 1950).

There is a copious bibliography dealing with different aspects of sexuality and reproduction in other mytilid species (CHIPPERFIELD, 1953; LUBET, 1959; SUGIURA, 1959; VELEZ & MARTINEZ, 1967; WILSON & HODGKING, 1967; PENCHASZADEH, 1971; VINUESA, 1978, etc.); however, studies about *Perumytilus purpuratus* are scarce, notwithstanding its importance as one of the principal components of littoral communities on exposed and semi-exposed rocky substrate. They refer preferably to ecological and developmental aspects (ZAIXSO & PASTOR, 1977; CORTÉS, 1979; HUBER, 1979; RAMORINO & CAMPOS, 1979).

It was important to know the reproductive habits to understand its population dynamics.

This paper presents the results obtained on its reproductive behavior, especially the sexual maturity cycle, sex ratio, spawning season and size at first maturity.

MATERIALS AND METHODS

A population of *Perumytilus purpuratus* of the intertidal zone of El Tabo, Chile (33°27' S; 71°41' W) was studied; samples were taken between October 1977 and December 1978.

Two samples were collected monthly, one for the macroscopic and biometric study of the gonads (A), the other one for their histologic study (B).

A) Macroscopic and Biometric Analysis of the Gonads.

One dm² of *Perumytilus purpuratus* was separated. The individuals were fixed in 10% formalin and later the following routine measurements were done:

Maximal length: measured from the shell's anterior end up to the posterior one, using a rule with a precision of 0.1 mm.

Sex: determined according to the mantle's color, females are brown and males yellow. In uncertain cases, sex was determined by examining a smear of the gonad.

Sexual maturity: expressed in stages of sexual maturity, according to a scale of sexual maturity detailed later.

Dry weight of soft parts: obtained on a Sartorius balance, keeping the samples at 110° C till constant weight was reached.

B) Microscopic Analysis of the Gonads.

Samples with a variable number of individuals (8-15) of minimal and median lengths of the population were selected to establish the state of sexual maturity of the population's most representative individuals and their minimal size at sexual maturity. Freshly collected samples were measured and separated by sex. A piece of the gonad was removed from the mantle's central sector. The pieces were fixed in Bouin's liquid for 8 hours, dehydrated in alcohol, imbedded in paraffin and stained with Haematoxylin-Eosin. Histological sections of 7 µm thickness were made with a Minot microtome. For microscopic observa-

tion a Leitz Ortholux was used and sections were photographed at a magnification of 100 and 250x.

To determine approximately the condition of sexual maturity of the population, in each sample analyzed, an average gonad index was calculated according to the method of SEED (1971).

Simultaneously, surface water temperatures were recorded in the vicinity of the collection area.

Scales of Gonadal Maturity

(Figures 1 and 2).

In order to establish the fluctuations of the gonadal cycle of *Perumytilus purpuratus*, a scale with the following stages of sexual development was prepared:

- Immaturity; stage before gametogenesis. Mantle transparent and thin. Neither the macro- nor the microscopic analysis of the gonads show differences between sexes, since only connective tissue with cells of different forms is observed.
- Initial maturity; stage of multiplication and cell arrangement. The mantle shows macroscopically a compact condition, due to an accumulation of gonadal products, which begin their invasion from the dorsal region. The mantle acquires the characteristic colors of each sex. Microscopic observation shows the cells of the connective tissue forming follicles, which at first are isolated, small and thick walled. Gonios and citos I can be distinguished in their interior; they are attached to the follicles's walls. The connective tissue, quite abundant at first, begins to decrease.
- Medium maturity; progressive gametogenesis stage. Macroscopically, the mantle is thicker than in the previous stage and the gonadal products cover it almost completely. Under the microscope, the follicles show thick walls and have grown in size and number, taking the place of the connective tissue, which continues decreasing with increasing maturity. The male follicles show a reduced lumen and a thick germinal layer, com-

posed mainly of spermatids. In females, oogonia and a large quantity of oocytes can be observed. The latter begin to invade the lumen of the follicles, being still attached to the follicles's wall by means of a stalk, which makes them appear pear-shaped.

- Maximal maturity; spermatogenesis and vitellogenesis stage: macroscopically, the mantle appears quite thick and turgescient, making more intense each sex color. Microscopically, a great development of the follicles is observed. Their walls are sharply defined and thin, and some of the follicles are fused. There is a great quantity of amoebocytes and scarce interfollicular connective tissue. On the wall of the male follicles, a few spermatogonia are observed, as well as a great quantity of spermatids and spermatozooids which occupy the whole lumen. The females show ripe oocytes, which tend to cluster freely and uniformly through the whole of the follicle's lumen, adopting a more globular shape. In some cases new developing oocytes are seen attached to the follicular wall. The spermatozooids, as well as the oocytes, are ready to be discharged.
- Partial discharge; stage of follicular emptying: due to the liberation of the gametes, the mantle appears macroscopically sparse, flaccid and thin. Microscopically, the follicles show torn and wrinkled walls. The male follicles contain amoebocytes, residues of spermatozooids and spermatids in different stages of reabsorption, others in full liberation of spermatozooids and still others empty and partially empty. The female follicles most often show disintegrating material. In both sexes regenerating zones are observed, the elements of which could be reabsorbed or could fully develop. In the interfollicular tissue there is a great amount of amoebocytes and an increase of adipose and connective tissue.
- Total discharge; maximal stage of disintegration. Macroscopically, the mantle is thin, flaccid, semitransparent and free of gametes. Microscopically, the follicles appear almost totally empty, contracted and with residues of disintegrating material. Only the presence of residual gametes allowed us to recognize the sex. Residues of gonadic tissue in gametogenesis are observed in others.

Explanation of Figure 1

Different stages of maturity of the male gonad of *Perumytilus purpuratus*. A and B - Medium maturity: thick germinal layer formed by spermatogonia, spermatocytes 1° and 2° and spermatids. C - Maximal maturity: there are principally spermatozoa, arranged radially in the follicles. D - Partial discharge: follicular emptying is initiated. E - Total discharge: contracted follicles, other follicles broken, residual spermatozoa.

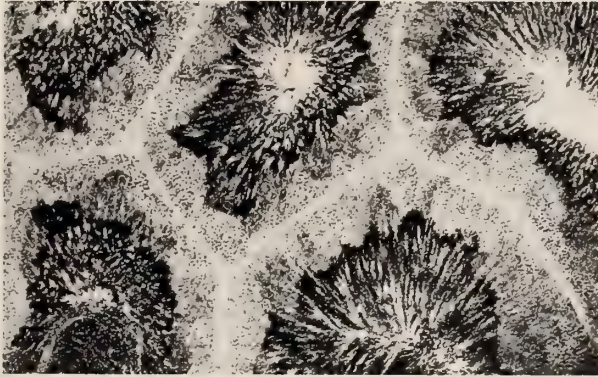


Figure 1a | 100 μm |

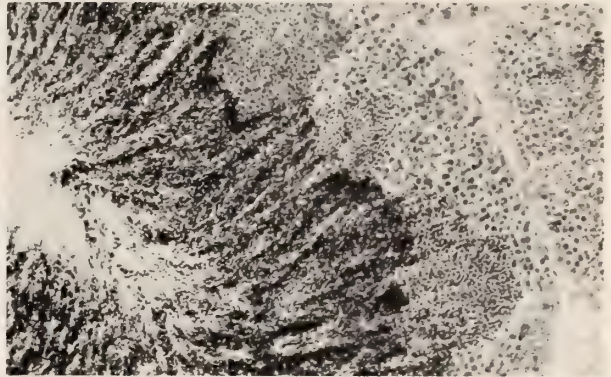


Figure 1b | 50 μm |

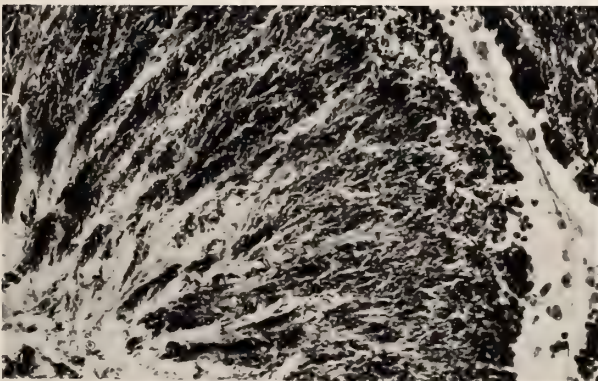


Figure 1c | 50 μm |



Figure 1d | 100 μm |

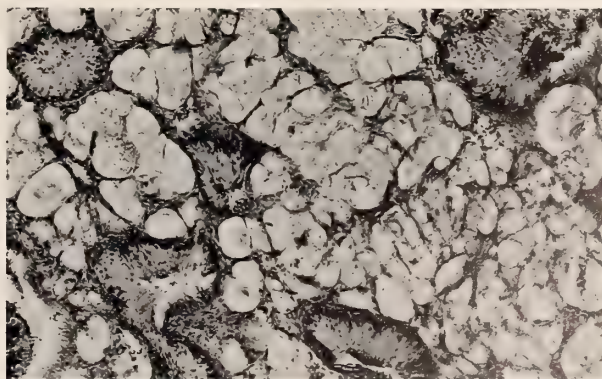


Figure 1e | 100 μm |

A great quantity of adipose and connective interfollicular tissue is present.

RESULTS

General Description of the Reproductive Apparatus.

The gonads of *Perumytilus purpuratus* are branched tubes, disseminated throughout mantle and mesosome. They are formed basically of follicles and connective tissue.

Males and females may be recognized macroscopically by the gonads' color once they have reached sexual maturity. With the increasing production of gametes, these invade the lobes of the mantle from the dorsal region to the ventral one. The mantle then acquires a yellow tint in the males and a brown one in the females, lighter or darker according to the number of spermatozooids and ovules. Microscopically, the sexes are distinguishable by their germinal cells, arranged radially inside the follicles.

Hermaphroditic individuals are occasionally found, showing one of their mantle's lobes with male and the other with female gonadic tissue.

Annual Cycle

The different stages of gonadic development, recognized through the histologic study of the gonads (Table 1) and the macroscopic and biometric analysis of them (Figure 4) show that the periods of growth, maturing and dis-

charge of gametes occur simultaneously in both sexes.

A period of maturity begins in April; the highest number of individuals at maximum maturity are recorded in July (Figure 4C); at the end of August this period attains the highest point; a large portion of the population discharging at that time (Figure 4D; Table 1). In September again a large number of individuals are noted in early and intermediate stages of maturing (Figure 4B), a fact suggesting the imminent start of another period of maturity in the population (with high values of maximum maturity in December and January). After spawning in August, the number of individuals in the discharging stage gradually increases, attaining its highest value in March. By this time half of the adult population is discharging, and the other half is already spent (Table 1).

The gonadic maturity is clearly revealed through the variation of the gonad index and the weight of the soft parts (Figure 5). The value of the latter increases simultaneously with the progressive development of gonadic tissue and they decrease in the period of gamete discharge.

Figure 5 also shows the variation of temperature, illustrating the fact that the predominance of individuals at the peak of maturity and discharge coincides with the increase in temperature.

Sex Ratio.

From 797 individuals examined between October 1977 and December 1978, 399 (50.1%) were females and 398 (49.9%) males.

Table 1

Distribution of the stages of gonadic development in the population of *Perumytilus purpuratus* at El Tabo, Chile. Histological analysis (N: total number of individuals, G.I.: gonadic index, %: frequency in %, %p: confidence limits).

	Total		Init. mat.		Med. mat.		Max. mat.		Part. evac.		Tot. evac.	
	N	G.I.	%	%p	%	%p	%	%p	%	%p	%	%p
29 Jan. 1978	15	2.53	6.7	0-32	33.3	12-62	53.3	27-79	6.7	0-32		0-22
26 Feb.	8	2.20		0-31		0-31	50.0	12-74	50.0	12-74		0-31
20 Mar.	8	1.50		0-31		0-31		0-31	50.0	12-74	50.0	12-74
1 Apr.	12	2.08		0-31	33.3	8-55	16.7	2-40	41.7	12-62	8.3	0-32
31 May	11	2.18	9.1	0-32	72.7	44-97	18.2	2-40		0-22		0-22
25 Jun.	10	2.60	10.0	0-45	30.0	7-65	60.0	26-88		0-31		0-31
31 Jul.												
30 Aug.	12	2.08		0-22	8.3	0-32	8.3	0-32	83.3	38-88		0-22
15 Sep.	8	2.25	37.5	7-65	25.0	3-56	25.0	3-56	12.5	0-45		0-31
17 Oct.	8	2.00		0-31	50.0	12-74		0-31	50.0	12-74		0-31
27 Nov.	10	2.20		0-31	60.0	26-88	20.0	3-56	20.0	3-56		0-31
28 Dec.	10	2.60		0-31	30.0	7-65	60.0	26-88	10.0	0-45		0-31

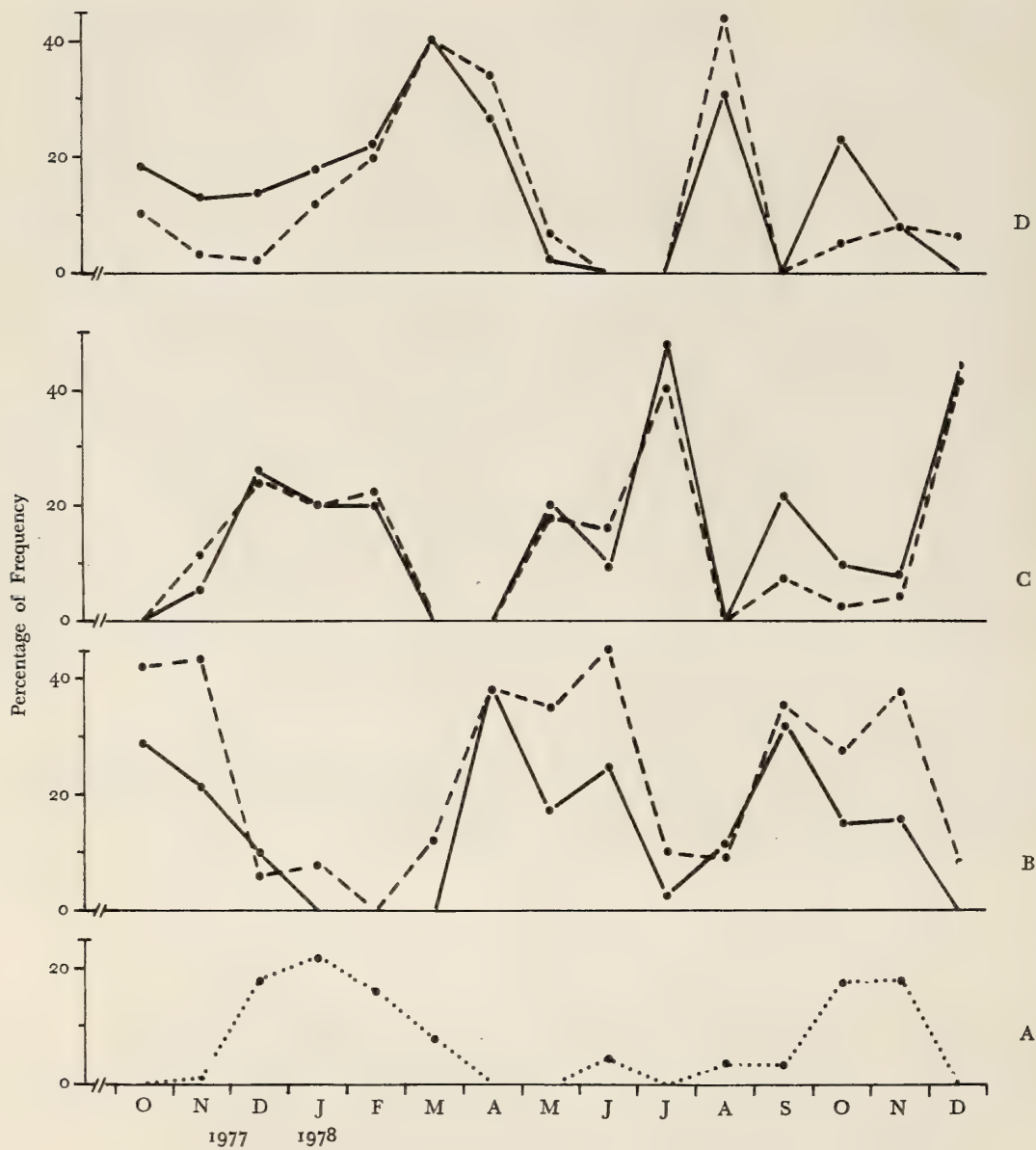


Figure 3

Percentages of individuals in different stages of gonadic development. A: immaturity; B: initial and medium maturity; C: maximum maturity; D: partial and total discharge.

♂: ———

♀: - - - -

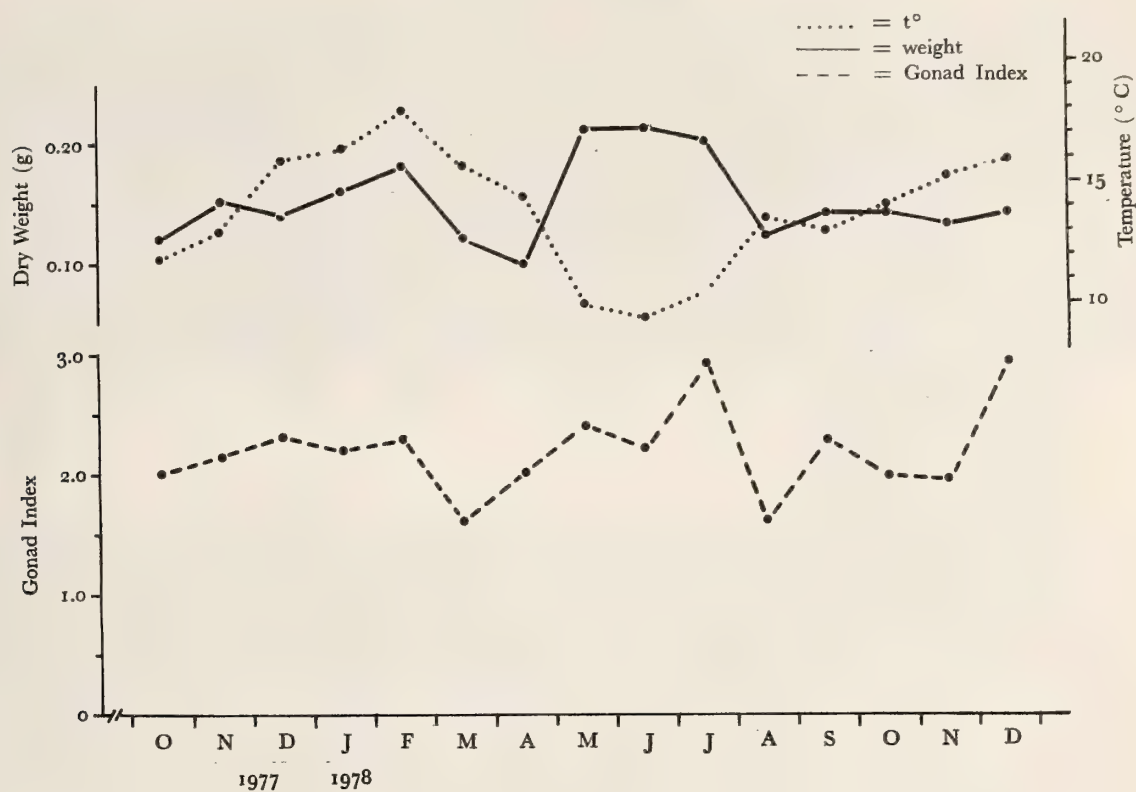


Figure 4

Seasonal variation of gonadic index (---), dry weight (—) of the soft parts of *Perumytilus purpuratus* and surface water temperature during the study period (.....).

Table 2

Sex ratio of monthly samples of *Perumytilus purpuratus* collected at El Tabo.

Month	Total N	Females		Males		x ²
		N	%	N	%	
23 Oct. 1977	38	18	47.3	20	52.6	0.10
27 Nov.	70	37	52.8	33	47.1	0.22
21 Dec.	68	36	52.9	32	47.0	0.23
29 Jan. 1978	53	28	52.8	25	47.1	0.17
26 Feb.	62	27	43.5	35	56.4	1.03
20 Mar.	77	35	45.4	42	54.5	0.63
1 Apr.	26	17	65.4	9	34.6	2.46
31 May	40	16	40.0	24	60.0	1.60
25 Jun.	42	15	35.7	27	64.3	3.40
31 Jul.	40	20	50.0	20	50.0	0.00
30 Aug.	83	50	60.2	33	39.7	3.48
15 Sep.	74	44	59.4	30	40.5	2.64
17 Oct.	33	19	57.6	14	42.4	0.75
27 Nov.	41	16	39.0	25	60.9	1.97
28 Dec.	50	21	42.0	29	58.0	1.28

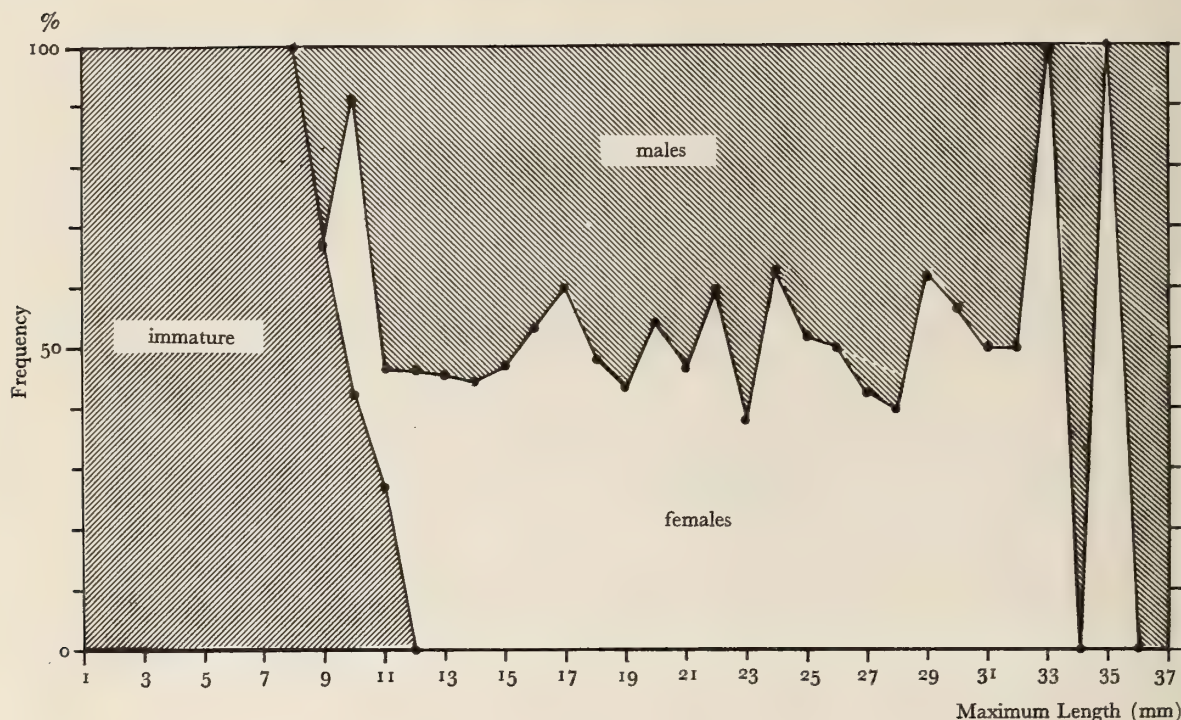


Figure 5

Ratio of sexes according to size (in %).

Sexual ratio is 1:1 (Table 2), and it does not vary with individual sizes from first maturity till adult size (Figure 5). The predominance of one or the other sex is due to the scarce number of specimens found over 33 mm, a fact that significantly affects sexual ratios.

Minimum Size at Maturity.

Table 3 shows the maximum lengths of immature individuals and the minimum lengths of mature specimens. These data indicate that the sexual maturity of *Perumytilus purpuratus* at El Tabo occurs from 8 mm to 10

mm of total shell length of the specimens. This corresponds to the first year of life, as it has been inferred from the data on the growth of the species (*in litteris*).

DISCUSSION

Gametogenesis in *Perumytilus purpuratus* presents the same phenomena observed in general in other molluscs. In their development the following stages are observed: periods of multiplication, growth, maturation and discharge. During the progress of gonadic development, the

Explanation of Figure 2

Different stages of maturity of the female gonad of *Perumytilus purpuratus*. A - Initial maturity: thick follicular wall and first signs of oogenesis, abundant interfollicular connective tissue. B - Medium maturity: more thick-walled follicles, oogonia and predominantly pedunculated oocytes. C - Maximum maturity:

oocytes freely distributed throughout the follicles. D - Partial discharge: follicles with residual oocytes and disintegrating material; other follicles with regenerating zones. E and F - Total discharge: follicles contracted, fused, broken, with disintegrating material; great quantity of amoebocytes and interfollicular adipose tissue.

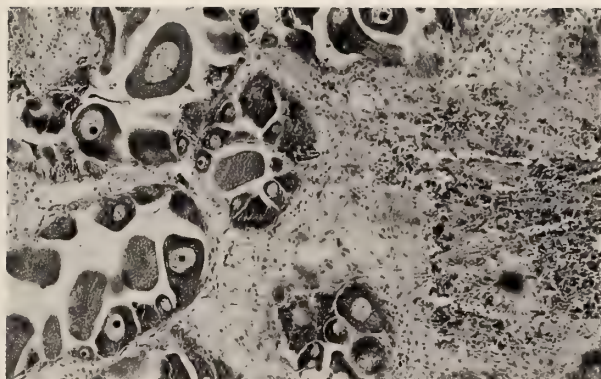


Figure 2a 100 μ m

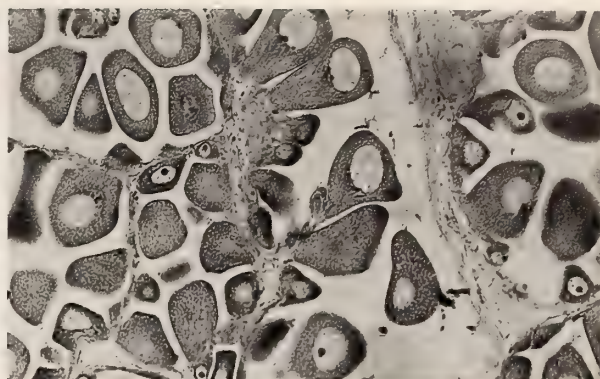


Figure 2b 100 μ m

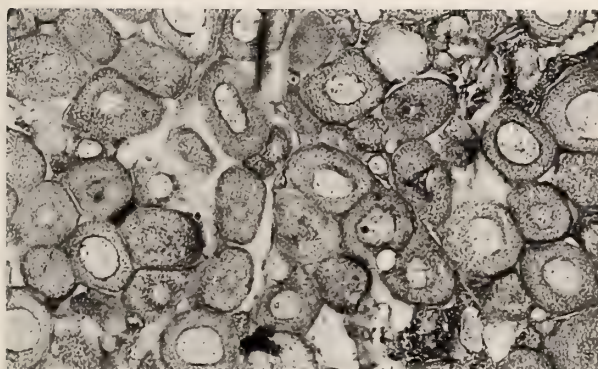


Figure 2c 100 μ m

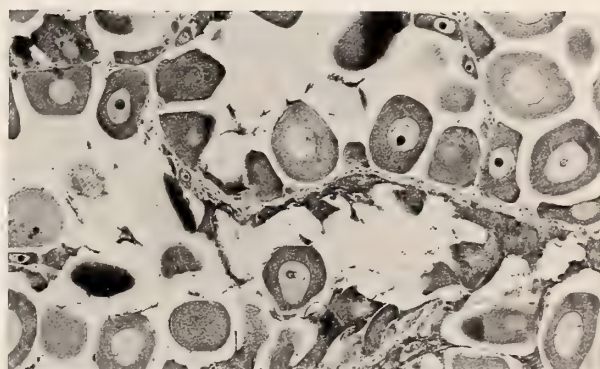


Figure 2d 100 μ m

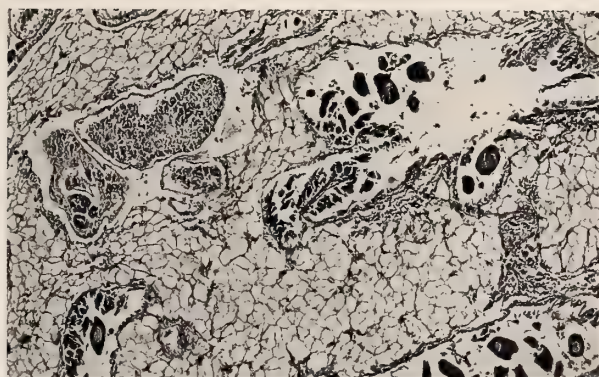


Figure 2e 100 μ m

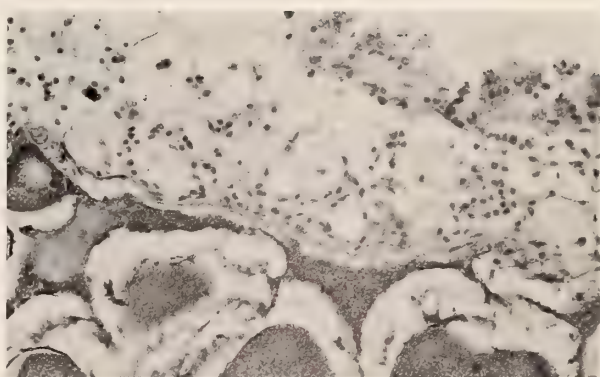


Figure 2f 100 μ m

Table 3

Maximum lengths of immature and minimum lengths at maturity of *Perumytilus purpuratus* in El Tabo (1977-1978).

Date	Immature Max. length (mm)	Maturity	
		Min. length (mm) female	male
23 Oct. 1977	—	19.2	13.0
27 Nov.	—	16.0	10.0
21 Dec.	9.3	8.0	11.0
29 Jan. 1978	—	23.3	21.0
26 Feb.	8.6	9.0	10.8
20 Mar.	6.5	12.0	13.0
1 Apr.	—	20.0	22.0
31 May	—	16.0	16.6
25 Jun.	7.0	17.2	14.5
31 Jul.	—	21.0	18.0
30 Aug.	8.0	10.0	8.0
15 Sep.	8.0	19.4	18.4
17 Oct.	10.0	10.7	18.0
27 Nov.	—	—	—
28 Dec.	—	16.0	15.1

follicles increase in number and size, whereas the intra-follicular connective tissue decreases.

Perumytilus purpuratus presents conditions of uniform maturity in the whole gonad, a phenomenon also observed in *Aulacomya ater* (CARREÑO & AVILÉS, 1977).

During the period of gonadic maturation, the first amoebocytes appear. These are cells rich in glycogen, abundant in the discharge period, disseminated throughout the whole gonadic tissue. These cells have also been observed in other molluscs carrying out different functions. LUNETTA (1969) found that during restoration of the follicles in *Mytilus perna*, these cells carry out a recuperation and reposition function of metabolites in the circulation. AVILÉS & LOZADA (1975), studying the gametogenesis of *Concholepas concholepas*, observed them attached to spermatozooids, suggesting a nutritional role. CARREÑO & AVILES (1977) in *Aulacomya ater* relate them to the growth and maturation of gametes as well.

Spawning individuals are present throughout the year, even if they are isolated and scarce between April and the first 15 days of August, not disturbing the total behavior of the population. The most important emissions of gametes at El Tabo's population occurred between the end of August and the beginning of April (spring and summer), showing two peaks, one at the end of August (1977), and another in March (1978). In 1962, the highest frequencies of spawning individuals were found in November and March (LOZADA, 1964) and at Antofagasta (23°40' S; 70°

25' W), in November and February (VILLALÓN, 1965), possibly happening earlier or later, depending on the influence of abiotic factors such as tides, salinity, temperature and others.

The reproductive tissue shows a marked gametogenic activity in some discharging individuals. The histological analysis of gonads in this stage showed the presence of regenerating zones in most of the examined samples. Although part of these elements in gametogenesis are reabsorbed, others continue their development, which explains the fast gonadic recuperation and the successive spawnings, preferably in males, which may be observed during spring and summer. Female maturity would be slower, due to an accumulation of stored reserves.

The presence of individuals in total spawning in March and April suggests a period of sexual rest, which would not involve the whole population—as it can be seen through the analysis of Table 2—or would be quite short, since the histological analysis reveals the start of another gametogenesis; at the moment, it is impossible to determine a well defined period of sexual rest, like the one found in *Mytilus edulis* and *Mytilus chilensis*.

It seems that spawning begins when the temperature increases. This relationship has already been observed in other mytilids like *Mytilus edulis* (SUGIURA, 1959; MOORE & REISH, 1968; SEED, 1971), *M. galloprovincialis* (SEED, 1971), *M. edulis chilensis* (PADILLA, 1973), *Aulacomya ater* (LOZADA, 1968), *M. edulis aoteanus* and *Aulacomya maoriana* (KENNEDY, 1977), and others, confirming the influence that water temperature exerts on the annual reproductive cycle. Its effect is significant, too, on the mytilids' fertilization and larval development, as it may be inferred from the works of BAYNE (1965) and LOOSANOFF & DAVIS (1951).

Perumytilus purpuratus reaches sexual maturity during the first year of life, approximately when it has grown to a length of 8-10 mm, as can be concluded from the data about population structure and the species' growth (in preparation).

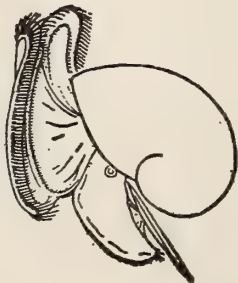
Thickness of gonads is not a trustworthy indicator of maturity, mature specimens with thin gonads having been observed, and vice versa. Therefore, it is necessary to complement those observations with a histological study of the gonads.

ACKNOWLEDGMENTS

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Range Extension and Notes on the Food, Morphology, and Color Pattern of the Dorid Nudibranch *Hallaxa chani*

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(1 Plate)

INTRODUCTION

Hallaxa chani GOSLINER & WILLIAMS, 1975 is an uncommon dorid nudibranch previously found only on the central and northern California coast. A total of 25 individuals have been reported in the literature, 21 by GOSLINER & WILLIAMS (1975), 3 by McDONALD & NYBAKKEN (1978), and 1 by JAECKLE (1981). Knowledge of the biology of *H. chani* is limited to the statement by McDonald & Nybakken that *H. chani* feeds on the colonial ascidian *Didemnum carnulentum* Ritter & Forsyth, 1917.

In the last five years I have found 8 individuals of *Hallaxa chani*: 6 in Santa Cruz County, California and 2 at Cape Arago, Oregon. These 8 individuals differed slightly from the original description of *H. chani* by GOSLINER & WILLIAMS (1975). Furthermore, 1 individual was found to be feeding on a sponge of the genus *Halisarca*.

The purpose of this paper is to record the range extension and new food record for *Hallaxa chani* and discuss the previous food record. I will also describe the morphological and color pattern differences between my specimens and Gosliner & Williams' specimens. An account of these differences is intended to supplement Gosliner & Williams' excellent original description of *H. chani* and thus help provide an indication of the variability in morphology and color pattern one can expect in *H. chani*.

RANGE AND COLLECTION LOCATIONS

GOSLINER & WILLIAMS (1975) reported *Hallaxa chani* from Tomales Point, Marin County, California (38°14'N; 123°00'W) to Shell Beach, San Luis Obispo County, California (35°12'N; 120°43'W), a distance of approxi-

mately 400 km. JAECKLE (1981) extended the range 320 km northward to Abalone Beach, Humboldt County, California (41°07'N; 124°09'W).

During a three year, monthly study (June 1975 to June 1978) of intertidal nudibranchs at Scott Creek Beach, Santa Cruz County, California I found 6 specimens of *Hallaxa chani* in the low intertidal zone. The study area at Scott Creek was on a large, gently sloping, rock shelf (composed of Santa Cruz mudstone) and contained many pools, ledges, and fissures. In the terminology of RICKETTS & CALVIN (1968), the Scott Creek rock shelf is classified as semi-protected outer coast. Scott Creek is well within the reported range of *H. chani*. The 6 Scott Creek specimens were found over a one year period (December 1975 to November 1976) in a relatively small area (400 m²), indicating that *H. chani* can be locally frequent for a certain time and absent (or very rare) in the same area at another time.

On March 15, 1980 and May 3, 1980 I found 2 individuals of *Hallaxa chani*, 20 mm and 28 mm long, respectively, in the low intertidal zone at North Cove, Cape Arago, Oregon (43°20'N; 124°22'W). This cove contains a mixture of sandstone ledges, shelves, and boulders of variable size and supports a diverse intertidal community. Protected by Simpson Reef, the north cove is classified as protected outer coast according to RICKETTS & CALVIN (1968). The March specimen was found on sponge on the underside of a slightly overhanging ledge, and the May specimen was found crawling in bright sunlight on red algae in the middle of a large shallow pool. Thin sections made of the March specimen revealed large, mature oocytes and spermatozoa in the ovotestis, indicating that *H. chani* is probably capable of reproducing at Cape Arago. The finding of these two specimens extends the range of *H. chani* northward approximately 250 km.

FOOD

I was able to collect food data on only 1 of the 8 *Hallaxa chani* that I have found. The individual of *H. chani* found at Cape Arago in March was found on a sponge of the genus *Halisarca*. It was not possible to identify the sponge to species—identification of the *Halisarca* species requires extensive life history data and is quite difficult (BERGQUIST, 1978; Hartman, pers. comm.).

I was not able to observe if the sponge had been grazed on, owing to its position under a ledge and the tide level (the sponge was partially submerged during a —0.15 m low tide).

In order to identify the sponge and determine if *Hallaxa chani* had been feeding on it, the nudibranch and a sample of the sponge were collected, fixed in Bouin fixative, embedded in paraplast, sectioned, and then stained with Mallory triple connective tissue stain. Examination of these sections revealed that *H. chani* was indeed feeding on *Halisarca*. The digestive gland of *H. chani* contained *Halisarca* spherulous cells (with their large, equal-sized vacuoles), aggregations of the thin fibrillar collagen of the sponge, clusters of choanocytes, and some unidentified *Halisarca* cells (see Figures 1 and 2). Neither spongin fibers nor spicules of any sort were found in the digestive system of the nudibranch. Nor was there any evidence of feeding on other types of organisms.

Further evidence that *Hallaxa chani* was feeding on *Halisarca* lies in the resemblance of *H. chani* to *Halisarca* in coloration and texture. Many eudoridacean nudibranchs closely match the color of their prey (THOMPSON, 1976; pers. obs.). This is thought to have protective value against visual predators, although there is little direct evidence for such value (THOMPSON, 1976). GARSTANG (1889) noted that some dorids also match their sponge prey in texture and hypothesized that this resemblance helps to further "deceive" a potential predator. I have not found any reference to Garstang on this point, nor

any later mention of the textural resemblance of some dorids to their prey. (However, FRETTER & GRAHAM, 1962: 557, note that many sponge and tunicate-feeding prosobranchs resemble their prey in both color and surface texture.) Many eudoridaceans do indeed have a texture similar to that of their sponge prey (pers. obs.)—largely a result of both having spicules. That the primary function of dorid spicules is to mimic sponge texture is debatable. Dorid spicules could also function in a more "active" defense role either by piercing a predator's tissues or, as PAINE (1963) suggested, by making the dorids more rigid and less easily swallowed.

The *Halisarca* on which *Hallaxa chani* was found was a yellowish-tan color and in the form of a thin blanketing sheet. The surface of the sponge was smooth and slick, yet quite firm to the touch. Like the other dendroceratid demosponges, *Halisarca* lacks spicules. The March specimen of *H. chani* was slightly brownish yellow in color; the May specimen was the same color. Furthermore, *H. chani* lacks the dorsal connective tissue spicules common to many dorid nudibranchs (pers. obs.). GOSLINER & WILLIAMS (1975) do not mention spicules in *H. chani* but state, "The dorsal surface is relatively rigid, but not scabrous to the touch."

In general, the color of *Hallaxa chani* longer than about 12 mm matches the color of *Halisarca* sp. Gosliner & Williams describe *H. chani* as being "... light lemon yellow with a darker hepatic region. Individuals less than 12 mm in length are generally light greyish to dull yellow. Larger individuals possess a richer yellow pigment. The entire dorsal surface contains reddish-brown flecks of variable shape and size. A series of larger dark brown maculations is distributed in the hepatic region." HARTMAN, in SMITH & CARLTON (1975), describes west coast *Halisarca* species as being "pale tan, yellow-tan, or light brown."

The only previous food record for *Hallaxa chani* is the statement by McDONALD & NYBAKKEN (1978) that "... 3 specimens of *Hallaxa chani* were found on the ascidian

Explanation of Figures 1 to 4

Figure 1: Transverse section (10 μ m thick) through portion of *Hallaxa chani* digestive gland showing *Halisarca* sp. spherulous cells (S), clusters of choanocytes (C), and a mass of fibrillar collagen (FC). The fibrillar collagen is in the digestive gland lumen. Spherulous cells are approximately 12 μ m in diameter. Bright field microscopy

Figure 2: Transverse section (8 μ m thick) through basal portion of *Halisarca* sp. showing upper portion of the basal mat of fibrillar collagen (BM), spherulous cells (S), and tracts of fibrillar colla-

gen (FC). Spherulous cells are approximately 12 μ m in diameter. Bright field microscopy

Figure 3: *Hallaxa chani* found on May 3, 1980 at Cape Arago. Dorsum is 28 mm long. The subcutaneous spots in the hepatic region of this specimen are quite faint, of irregular size and shape, and not paired

Figure 4: *Hallaxa chani* found on March 15, 1980 at Cape Arago. Dorsum is 20 mm long. The subcutaneous spots in the hepatic region of this specimen are dark, of irregular size and shape, and incompletely paired. Some small air bubbles are on the dorsum

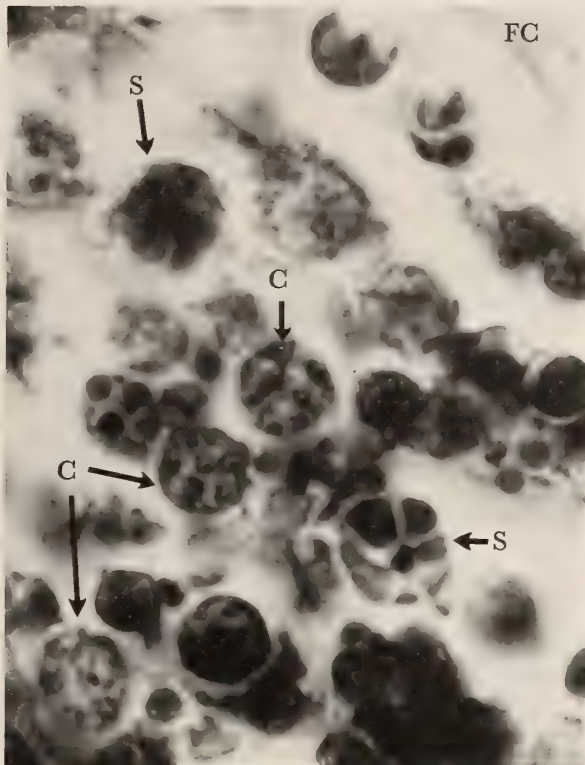


Figure 1

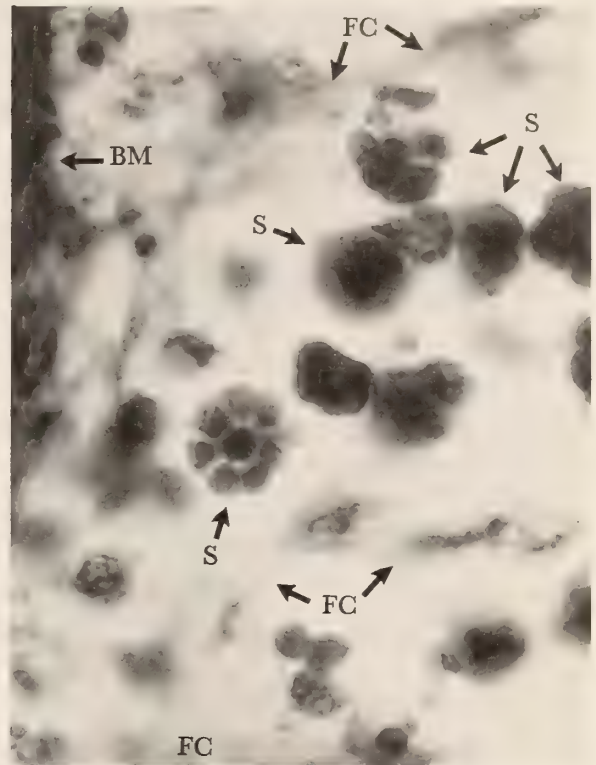


Figure 2



Figure 3



Figure 4

Didemnum carnulentum Ritter & Forsyth, 1917. The nudibranchs had grazed large portions of the ascidian." This food record requires further verification for a number of reasons: 1) McDonald & Nybakken did not actually observe feeding, nor did they examine gut contents of *H. chani*. 2) *H. chani* is a eudoridacean—as far as I know, all eudoridaceans feed on sponges (BLOOM, 1976; McDONALD & NYBAKKEN, 1978; THOMPSON, 1964 and 1976a). In connection with feeding see 5) below. 3) The color of *Didemnum carnulentum* is dense white to pinkish-white (SMITH & CARLTON, 1975). Larger *H. chani* are yellowish in color (see above) and thus would not resemble their prey as do many other northeastern Pacific eudoridaceans; there are, however, some notable exceptions such as the *Cadlina* species. It is possible, though, that smaller individuals of *H. chani* match *Didemnum* quite well. 4) *Didemnum carnulentum* is "abundant" (SMITH & CARLTON, 1975), while *H. chani* and *Halisarca* are quite rare. If *H. chani* fed on *Didemnum* one might expect *H. chani* to be more abundant. 5) The radula of *H. chani* is very different from the radula of other colonial ascidian-feeding gastropods such as the dorid nudibranchs *Goniadoris nodosa* (Montagu, 1808) and *Acanthodoris nanaimoensis* (O'Donoghue, 1921) and prosobranchs of the family Lamelliariidae (see THOMPSON, 1976b for scanning electron micrographs of the 2 dorid radulas and BEHRENS, 1980 for drawings of Lamelliariidae radulae). Indeed, the feeding method of *H. chani* is probably very different from the feeding methods of gastropods known to feed on colonial ascidians. *Goniadoris nodosa* and *Acanthodoris nanaimoensis* are suction feeders which use the radula mainly to rasp a hole in the ascidian test. Soft parts of the ascidian are then sucked out as a result of buccal bulb contractions (FORREST, 1953; MCBETH, 1971; THOMPSON, 1976). Members of the Lamelliariidae (and some of the Triviidae and Cypraeidae) feed on ascidians with the aid of the radula mounted inside the end of a proboscis (FRETTER & GRAHAM, 1962). Fretter & Graham do not mention if any suction is employed by the Lamelliariidae in moving food up the proboscis. As far as I know, all colonial ascidian-feeding gastropods utilize either suction or a fairly long proboscis in feeding (FRETTER & GRAHAM, 1962; HYMAN, 1967; THOMPSON, 1976). I do not know if *H. chani* is capable of suction feeding, or how extensible its radula is. In the eudoridaceans a proboscis is lacking, and pieces of food are moved into the esophagus primarily by the action of the radula (THOMPSON, 1976)—this type of feeding may not be efficient on colonial ascidians. However, it is interesting to note that some colonial ascidians have a form and external texture similar to that of *Halisarca* and other demosponges—the two types of organisms may be similarly vulnerable to predation by *H. chani*.

BERTSCH (1980) states that the radular morphology of

Hallaxa chani is "distinctly different" from the radular morphology of the other eudoridaceans listed by McDonald and Nybakken (1978) and implies that it is not surprising that *H. chani* "feeds on tunicates" (or at least some non-sponge organism). As I will mention in a forthcoming paper, the radula of *H. chani* is quite similar to the radula of other dorids which feed exclusively on non-spiculate demosponges of the orders Dictyoceratida and Dendroceratida. The radulae of these dorids are typically very small and possess a preponderance of thin, knife-like teeth with serrate or pectinate denticulation and reduced cusps. Dorids which feed on spiculate sponges (particularly sponges possessing highly reticulated spicules and spongin fiber skeletons) typically have large radulae with smooth or denticulate, hook-shaped teeth (YOUNG, 1969; BLOOM, 1976; BERTSCH, 1980; see drawings of various dorid radulae in MACFARLAND, 1966; and see McDONALD & NYBAKKEN, 1978, for food records).

As far as I know, *Hallaxa chani* is the first dorid to be reported feeding on a sponge which lacks both spicules and spongin fibers. However, *Halisarca* does have tracts of fibrillar collagen which no doubt are similar in function to spongin fibers. Furthermore, tracts of fibrillar collagen may present similar cutting, rasping, ingestion, and digestion problems to dorid feeding apparatuses and digestive systems.

Further laboratory and field observations of feeding by *Hallaxa chani* are needed to determine the major food(s) of *H. chani*, its feeding method, and to determine if *H. chani* actually feeds on colonial ascidians. There may be geographic and (or) age-specific differences in feeding by *H. chani*.

COLOR PATTERN AND MORPHOLOGY

GOSLINER & WILLIAMS (1975) describe "paired, dark sub-cutaneous maculations on both sides of the hepatic region" in *Hallaxa chani*. Furthermore, their figures of *H. chani* show these maculations to be round or oval in shape. With the exception of the two sub-cutaneous spots directly anterior to the branchial plumes, the sub-cutaneous spots were either never paired or were only very roughly paired in all of the specimens I have examined (see Figures 3 and 4). Furthermore, the sub-cutaneous spots were usually quite irregular in shape. Occasionally there were also some smaller, lighter, sub-cutaneous maculations in the center of the hepatic region. Gosliner & Williams note that the two spots just anterior to the gills are usually darker than the other spots—this was true for all the individuals I examined.

All of the *Hallaxa chani* I have found fit the rest of the color description given by Gosliner & Williams. The

smaller specimens were a dull, light greyish yellow, while the larger specimens were a richer, darker yellow. All of the specimens had reddish-brown flecks of variable size scattered over the entire dorsum.

The branchial plumes of the individuals I observed were composed of 11 to 15 unipinnate gills—Gosliner & Williams reported 12 to 14 gills. Gosliner & Williams also stated that the branchial sheath can extend one half the length of the extended gills. The maximum branchial sheath height I observed was about one third the height of the gills.

According to Gosliner & Williams the rhinophores of *Hallaxa chani* have 8 to 10 lamellae, and the rhinophore sheath can extend almost one half the length of the extended rhinophore. I have observed 9 to 12 lamellae, and that the sheath extends up to one quarter the height of the rhinophores. However, the rhinophore sheath can extend somewhat higher when the rhinophores are partially retracted. The rhinophore sheath was always much closer fitting than the sheath pictured in figure 3a of Gosliner & Williams' paper. Gosliner & Williams noted that the rhinophores of *H. chani* have maroon colored tips. With the exception of one Scott Creek specimen, all of my specimens of *H. chani* had maroon-tipped rhinophores. The rhinophores of the exceptional specimen (which was 10 mm long) were completely light yellow.

Figures 1 and 3a of Gosliner & Williams' paper are not accurate with respect to the rhinophore lamellae (leaflets). Their drawings depict the lamellae as being continuous around the anterior side of the rhinophores (*i.e.*, that the rhinophores are almost completely perfoliate). In every specimen of *Hallaxa chani* I have found, I have observed that the lamellae are divided anteriorly by a longitudinal septum—that is, there are two sets of lamellae per rhinophore. Thus, the rhinophores resemble the bipectinate gills of some prosobranchs and are very similar in form to those of some other dorids such as *Doriopsilla albopunctata* (Cooper, 1863) and *Anisodoris nobilis* (MacFarland, 1905) (see plate 29 in MacFarland, 1966).

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Notes on the Reproductive Biology and Behavior of the West Indian Fighting Conch, *Strombus pugilis* Linnaeus in Barbados, with Evidence of Male Guarding

BY

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(1 Text figure)

INTRODUCTION

EXISTING INFORMATION on the reproductive biology and behavior of the West Indian fighting conch, *Strombus pugilis* Linnaeus, 1758, is limited. PERCHARDE (1970) reported that in Trinidadian waters three colonies of fighting conchs moved downslope and buried themselves, with apparent sex segregation, in November 1967. They did not return to normal feeding and behavioral patterns until March/April 1968. Then the males emerged and commenced feeding but the females, all of which were solitary, simultaneously engaged in egg-laying before emerging to feed. He suggested that copulation, which had not been witnessed, and fertilization occur within a short time period and might be lunar related. BROWNELL (1977) in Venezuela found from diving observations, which averaged twice per month from July 1975 to June 1976, that *S. pugilis* spawned from March to May. He also noted that all egg-laying females were solitary. However, both RANDALL (1964) in the U.S. Virgin Islands, and Brownell have reported that ovipositing females of *Strombus gigas*, the queen conch, were often accompanied by one to three males, sometimes with concurrent copulation.

This study reports in detail on the reproductive behavior of *Strombus pugilis* in Barbadian waters. Additional

information on their fecundity and apparent spawning cycle is supplied, with new evidence supportive of combative tendencies in the males. All research was carried out in Barbados, West Indies, at the Bellairs Research Institute of McGill University during the period May 1979 - October 1980.

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DESCRIPTION AND LOCATION OF STUDY SITES

The principal study site was located 200 m offshore and 50 m north of the mouth of the Holetown River, St. James Parish, Barbados. The colony inhabited an area of sandy-mud in 5-8 m of water, where the bottom sloped to sea-

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ward at an angle of approximately 10° . Two secondary sites were also established on the west coast in 8-10 m water depths. One colony was approximately 600 m north of the principal site and separated from it by two coral reefs. The other was several kilometers to the north at Speightstown, St. Peter. Both secondary sites had sandy-mud bottoms with no appreciable slope.

MATERIALS AND METHODS

Field Materials and Methods

On November 1, 1979, divers at the principal site measured, sexed, tagged and released 33 adult conchs *in situ*. These tagged conchs constituted a sub-sample from a large colony of approximately 500 individuals inhabiting a surveyed grid area of 300 m^2 . This site was visited 17 times from November 1 to December 16, 1979. During each visit the entire grid plus an additional 5 m on the periphery were surveyed for tagged animals. When conchs were encountered their exact location in relation to the grid was determined, their ongoing behavior recorded and the main activity of the entire colony noted. In the periods May-September 1979 and January-October 1980, only the main activity of the colony was noted. Temperature and salinity of the bottom waters at this site were monitored October 1979-October 1980.

Untagged colonies at the secondary sites were visited occasionally from May to December 1979.

Laboratory Materials and Methods

In July 1979, a cement water table (3 m x 1 m x 26 cm) was filled to a depth of 6 cm with sediment from areas in the field inhabited by *Strombus pugilis*. This muddy sand was then overlain with 1 cm of beach sand to help maintain water clarity. The water table was supplied with running seawater averaging 28.1°C pumped directly from an intake 25 m offshore. On July 17, 35 adult *S. pugilis* were collected by divers from the bay at Holetown. Four of the 20 females collected were in the process of egg-laying.

All conchs were maintained overnight in three 40 L aquaria supplied with running seawater. Measurements and sex determinations were made the next day. The animals were then tagged with numbered squares of buoyant polyethylene tied to 6 cm lengths of dental floss.

These were attached to the conch shells between two dorsal spines on the penultimate whorl (Barbadian *Strombus pugilis* lack spines on the body whorl) with a rapid-drying adhesive. These conchs, plus 10 others from the Speightstown site which had been treated similarly 3 weeks previously and exhibited no harmful side-effects, were then placed in the prepared water table for observation over a period of 4 months. Various algal species scraped from hard surfaces in the intertidal zone were added periodically to the water table and were accepted by the conchs as food items.

The laboratory population density of approximately 14 conchs per square meter was similar to densities obtained in censuses of field colonies actively engaged in reproduction or feeding, or both. The laboratory population was 58% female, which was similar to the composition obtained in field studies.

LABORATORY RESULTS AND OBSERVATIONS

Egg-laying, Copulation and Associated Pairs

The laboratory colony was observed July 18-November 15, 1979. The first egg mass was produced on July 19 at 1400 h by a female accompanied by a male positioned posteriorly and on her right side. Their shells formed an angle of approximately 60° , with the male's propodium touching the shell lip of the female. The male remained inactive while the female deposited the egg strand. As the egg mass increased in length, it was occasionally pushed away to the right of the female by her propodium; a behavioral pattern similar to that described for *Strombus costatus* (BERG, 1974). Thus, the two partners remained stationary as the egg mass was produced. (This behavior is contrary to that observed by Percharde; *i.e.*, buried, solitary, egg-laying females in Trinidad, 1970). This association of the male and female continued undisturbed until sometime after 1845 h when they were last observed together. The female finished the egg mass sometime between 2030-2230 h. It is not known whether she was alone during the last few hours of ovipositing. Copulation prior to this egg-laying was not observed and may have occurred in the laboratory and/or in nature. The eggs of this female and those subsequently laid by all other females in the laboratory produced viable embryos which hatched within 3 to 5 days. During that same day, several solitary females were observed laying eggs.

A brief period (5 days) of intense reproductive activity ensued in the laboratory colony. Copulation with non-egg-laying females was observed 15 times and with ovipositing females 6 times, and 12 associated pairs were studied. All conchs remained on the sand surface until 2100-2230 h on July 23 when 5 conchs buried themselves. By 1900 h on July 24, 44 of the 45 tagged animals were completely buried with only their eyestalks and some spine tips visible. Thirty-one of the 34 egg masses produced were ascribed to 20 specific females, therefore averaging a minimum of 1.6 egg masses per female in a 5-day reproductively-active period. Records were not kept of the percentage of egg-laying time that ovipositing females were solitary.

Male Guarding and Fighting

Initially it was thought that the male attending an ovipositing female might be protecting her from predation while she was fully exposed and stationary on the substrate surface. However, on July 22 at 1050 h the significance of this guarding behavior of the male *Strombus pugilis* became apparent.

A female was engaged in egg-laying and two males were positioned with their anterior ends close to the female's flared shell lip. Neither male was engaged in copulation but one was touching the outside of the female's shell lip with his propodium. The males began to 'spar' with each other using the radulae and jaws on their extended proboscises. When one retracted his proboscis, the more aggressive conch (in this case, the conch not touching the female) jabbed under the shell of the other with his proboscis at the eye and tentacle region of the retracted conch. After receiving several of these jabs, the less aggressive conch, with its soft parts retracted under its shell, moved off of the female, became quiescent for several minutes, then moved away. The victor then copulated with the female and assumed what apparently is the guarding stance of touching her shell lip with his propodium. Within a few minutes of copulation the new male guard successfully defended his position in similar fashion from take-over by a new male. Males that actively attempted to copulate with a guarded female or to displace her male guard are referred to here as 'primary' suitors (Figure 1). During this entire sequence of events, the female continued to lay eggs uninterrupted.

This behavior pattern was subsequently observed several times in other groups in the water table. These groups were composed of two to four conchs: one egg-laying

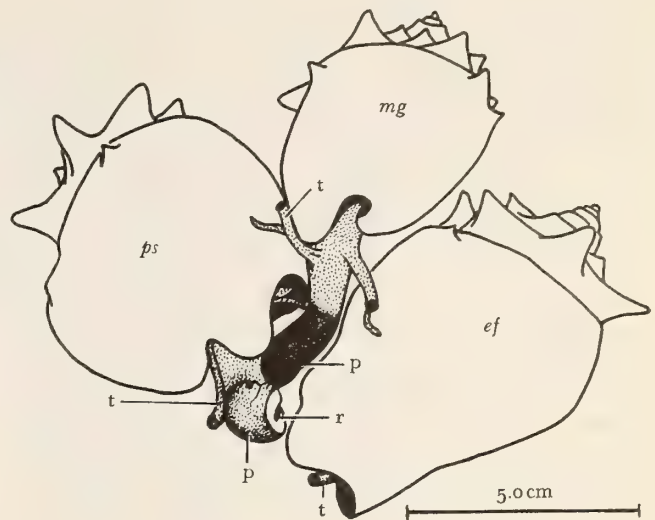


Figure 1

CONCH FIGHTING

Two male *Strombus pugilis* fight – one to remain and the other to become the male guard of the egg-laying female. (The emerging egg mass is not shown, but would be along her right side, on the sediment surface.) mg – male guard; ps – primary suitor (see text); ef – egg-laying female; p – proboscis; r – radula; t – tentacle-bearing eyestalk

female, her male guard and usually one but sometimes two primary suitors. Occasionally a third or fourth male, here designated as 'secondary' suitors, was present. These secondary suitors had no physical contact with the female nor with her male guard but would remain very close to a mated pair, albeit inactive, for long periods. They displayed no other behavior that could be described as a form of active pursuit of the female.

When two or more females were ovipositing close to each other, larger aggregates of conchs resulted and the activity level amongst the males was high. One such grouping consisted of 19 conchs, which were either touching or within one conch-length of another individual. Aggregates of this type of up to 30 conchs were also observed in the field colonies. The exact sexual makeup of these aggregates was not recorded in any observation; however, in the laboratory aggregates every ovipositing female was guarded and several primary suitors were seen moving

within the large groupings. Non-egg-laying females feeding in the vicinity tended to continue moving past the aggregates.

The observed associations between an ovipositing female and a male guard were maintained either until the female finished egg-laying (at which time she abruptly leaves) or until the male was displaced by another male. Except when under attack, a male guard was never observed to leave an egg-laying female. In one case the guard remained for at least 8½ hours. During these associations repeated copulations between the same partners were observed but copulation was not a continual process and was never observed immediately prior to the female's departure.

Combat between males when neither was touching a female was observed twice. In one case a male guard entered into combat with a secondary suitor only after the female had abandoned her recently deposited egg mass. In the other instance, two primary suitors engaged in combat while near a male guard copulating with his ovipositing female.

Females did not engage in combat. Often a feeding female approached a guarded ovipositing female but no aggression was noted on either the part of the male guard or of the females; nor did the male guard abandon the ovipositing female to pursue the passing female.

Copulation with non-egg-laying females occurred frequently in the laboratory population but no fighting over these females was observed. In one instance a non-egg-laying female was seen with the verges of two males inserted under her shell lip, one anteriorly and the other from the more usual 60° angle. No fight resulted between these two males.

Seven fights were observed before 99% of the conchs buried themselves on July 24.

Attenuation of Activity in the Laboratory Colony

Two additional periods of intense reproductive activity occurred in the laboratory colony within the next two weeks; one of 4 days duration from July 26 to 29 and the other of 2 days on August 7 and 8. In total, 32 egg masses were produced and 17 copulations with non-egg-laying females, 13 with egg-laying females, 15 associated pairs and 5 fights were observed. After August 8, the laboratory conchs remained buried most of the time except when fresh algae were added to the water table. Only one reproductive act was observed between August 8 and November 15 (when all observations were terminated) and that was a single copulation involving a non-egg-laying female on August 26; the female did not subsequently oviposit. PER-

RON (1978) reported a similar reduction of surface activity as the length of time retained in the laboratory increased for specimens of *Aporrhais occidentalis* (Superfamily Strombacea).

FIELD RESULTS AND OBSERVATIONS

Egg masses were seen at at least one of the three sites each month from May 1979 to October 1980, except March 1980 at which time only the tagged colony was under observation. At times of intense reproductive activity all sites revealed groups of conchs varying in number from 2-30 individuals, as well as some solitary egg-laying females. No correlation of their reproductive, burying or feeding activities with lunar phases was evident.

The tagged colony showed some evidence of a cyclic behavior pattern, however, with individuals alternating between buried and surface-active periods. Table 1 lists the main ongoing behaviors of the Hometown colony at each visit. In early October 1979, the colony exhibited a period of intense reproductive activity. By late October individuals were more dispersed and actively feeding on the sediment surface. By mid-November very few were feeding, minimal reproductive activity was noted and many were buried. This condition remained extremely stable through to mid-December as shown by one tagged individual which was found in exactly the same location for three consecutive weeks, feeding on the sediment surface while buried. By late December more individuals were emerged and feeding and the presence of one egg mass was noted. No further observations were made until January 26, 1980, when most animals were actively feeding and a few females were laying eggs. Intense reproductive activity was observed on the 1ST and 23RD February. No conchs were seen on the surface on March 1, nor were any tags visible. Heavy seas which stirred up the bottom sediments on February 28 and 29 may have caused this disappearance of the colony. It is presumed that they were in the grid area but buried with their tags covered by the settled sand and silt because their previous greatest migration from the grid site had been 25 m and this additional distance was searched on March 1 without locating them. On April 12, they were again feeding within the grid area but by April 29 intense reproductive activity was evident. Feeding, egg-laying and copulating were the main activities observed on the May to October 1980 dives except on July 12 when many buried conchs were noted.

Two conch fights involving male *Strombus pugilis* were seen *in situ* in the tagged colony. These fights were similar to those observed in the laboratory.

Table 1

Main activity of the *Strombus pugilis* colony at Holetown, Barbados, October 1979-October 1980

Year	Time	Date	Main activity	Year	Time	Date	Main activity
1979	1100	Oct. 2	F, (M)	1979	1030	Dec. 7	B
	1100	Oct. 3	E		1100	Dec. 10	B, (F)
	1300	Oct. 5	F, M		1100	Dec. 11	B, F
	1400	Oct. 6	F, M		1100	Dec. 13	B, F
	1100	Oct. 9	F, (M)		1100	Dec. 16	B, F
	1400	Oct. 10	F	1980	1100	Jan. 26	F, (E)
	1400	Oct. 13	F, (E)		1100	Feb. 1	E
	1500	Oct. 28	F, (M)		1100	Feb. 23	E, M
	1200	¹ Nov. 1	F		1100	Mar. 1	B presumed ²
	1400	Nov. 8	B		1100	Mar. 24	F, B
	1300	Nov. 9	B		1100	Apr. 12	F
	1000	Nov. 12	B		1100	Apr. 29	E
	1300	Nov. 17	B		1100	May 13	F, M
	1400	Nov. 18	B		1100	May 30	E
	1100	Nov. 20	B		1100	June 28	E, F
	1100	Nov. 24	B		1100	July 12	F, B, M
	1030	Nov. 27	B		1100	July 28	E, M
	1430	Dec. 1	B, (F)		1100	Aug. 10	F, E, M
	1630	Dec. 5	B		1100	Sept. 25	E, M
	0830	Dec. 6	B		1100	Oct. 23	E, M

¹ = tagged *in situ*² = see text for explanation

B = buried conchs; F = feeding conchs, exposed on the sediment surface; E = egg-laying activities, with fresh egg masses on the sediment surface; M = abandoned egg masses on the sediment surface; () = this activity noticeable but not a main activity of the colony.

Sex segregation in burying was not apparent nor was there any appreciable migration up- or downslope as had been observed by Percharde in Trinidad. However, there was evidence of migration of the colony north and south along the 5-7 m depth contour in October, November 1979 and February, May, July, August and September 1980. The migration range was approximately 60 m; the greatest distance covered by the colony between successive observations was 30 m.

During a period of very heavy rainfall and freshwater inundation of the principal site's surface waters in November-December 1979, bottom temperatures did not fluctuate by more than 0.5° C and bottom salinity was stable to within 0.5‰ of the annual mean of 34.7‰. Mean annual bottom temperature was 27.6° C. In view of this apparent stability even during periods of heavy run-off, local rainfall was not further considered as having a direct influence on the conchs' behavior.

DISCUSSION

Surface Activity Cycle

The field and laboratory observations indicate that *Strombus pugilis* in Barbados engage in reproductive activity, to some extent, on a year-round basis. In addition, they have an apparently cyclic behavior affecting reproduction which seems to consist of the following generalized stages in order: (i) burying, with highly localized feeding; (ii) emergence, with feeding on the sediment surface over greater distances; (iii) one or more periods of intense reproductive activity in pairs or aggregates; (iv) dispersal into the surface feeding pattern, followed by either (i) or (iii).

The greatest numbers of conchs were seen on the surface in August-September of 1979 and 1980 and the least numbers in November 1979 and March 1980; the number

on the surface at other times varied between these two extremes. Therefore, for much of the year this activity cycle may not be followed rigorously by all members of the population at any one time.

The attenuation of reproductive activity of the laboratory population indicates that the control(s) over levels of surface activity of these animals is (are) exogenous.

An Interpretation of the Male Guarding and Fighting Behaviors

The observance of male guarding and conch fighting in the wild colony indicates that the behaviors are elements of the natural behavioral repertoire of *Strombus pugilis* and not artifacts induced by laboratory confinement. These behaviors can be interpreted as tactics of the male reproductive strategy. To assure paternity, the male *S. pugilis* may (i) copulate with any available female even if she is not ovipositing; (ii) copulate with an ovipositing solitary female and then guard her as she continues to deposit her eggs; (iii) attempt to displace a male guard and if successful, immediately copulate with the female, remaining with her until ovipositing is completed or until he is in turn displaced; (iv) engage in multiple inseminations with the female he is guarding. Of these 4 tactics, the 3 which involve male guarding and fighting tend to limit female promiscuity and may confer an advantage towards successful paternity for the male guard.

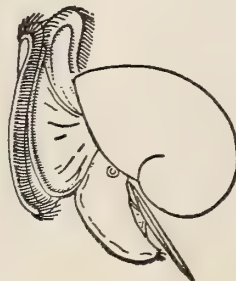
Male guarding behavior is not new to the animal kingdom but it is reported here for the first time for *Strombus pugilis* Linnaeus. It was very appropriate, therefore, that this animal was so named. Literally translated, *Strombus pugilis* means 'boxing spire' and was intended as a description of the animal's active nature when handled (DODGE, 1956; 1959). It is fitting then, that this is the first

species of this genus for which combative tendencies have been recorded.

Although analagous behavior has not been observed in any other member of the Superfamily Strombacea, its members are noted for their similarity in other behaviors (notably leaping, escape response and normal locomotion) and morphology (BERG, 1974). Furthermore, it has been noted that members of the *Strombus* genus generally congregate in large colonies to spawn (ABBOTT, 1960) and *S. gigas* has been observed spawning in groups consisting of 1 female and 2 to 3 males (RANDALL, 1964), as does *S. pugilis*. Future careful observation of other species may reveal the widespread occurrence of male guarding and fighting behaviors within the genus and perhaps within the Superfamily.

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Rhizochilus in the Gulf of California

(Neogastropoda : ? Coralliophilidae)

BY

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A BLACK CORAL OF UNDETERMINED SPECIES belonging to the sub-order ANTIPATHARIA has been brought in for many years by divers and fishermen to Guaymas, Sonora, Mexico. Recently, collectors have found a gastropod living on the base of the coral. The shell morphology and mode of living are unusual and place the species in the genus *Rhizochilus* Steenstrup, 1850.

The type locality for *Rhizochilus antipathus* Steenstrup, 1850, is in the Red Sea. Additional records are rare. One lot in the National Museum of Natural History - Smithsonian Institution was taken from the Island of Rodrigues, Indian Ocean. The genus is also reported from the Marquesas Islands by Dr. Harald Rehder (personal communication to Dr. Joseph Rosewater). KAY, 1979, reports *Rhizochilus* from the Hawaiian Islands; but her illustration shows significant differences from the west Mexican material. So do illustrations by H. & A. ADAMS, 1853, and GRAY, 1851 (both repeated in TRYON, 1880).

Thirteen lots of material from the Gulf of California have been examined. These lots were all taken in 20-60 m along the Sonoran coast, except for 3 lots found as beach specimens near Cabo Haro. Each lot consists of a coral base with 1-6 individual shells attached. Most, even the very young (6 mm), are grouped close together, with the young on top of mature shells and each covered with coral except for the end of the anterior canal. The coral is laid down in thin layers that remain pliable and separable while in sea water.

Several characteristics of this species have not previously been described or are different from those of *Rhizochilus antipathus*. The protoconch is narrowly turbinate, of 3 whorls, the 1st minute and unornamented, the 2nd and 3rd with 1 and then 2 spiral cords made nodose by numerous weak axial ribs. This protoconch is very similar to that

of *Quoyula madreporarum* (Sowerby, 1834). The teleoconch begins with only a slight change of color and increases regularly up to the body whorl, which is greatly inflated posteriorly, resulting in a deeply canaliculated suture. The anterior canal is long and closed with thin white shelly material, sometimes growing longer than the spire and body whorl combined. Often, the only visible sign of a subsurface shell is the open end of the canal rimmed with living coral. When the coral is removed to expose the tan shell, there may be a thick irregular rim of shelly material around the aperture, perhaps extruded by the animal in an effort to lift off the substrate and to withstand the constriction of the overlying coral. This may also be a mechanism enabling the animal to excrete excess calcium resulting from its coral diet.

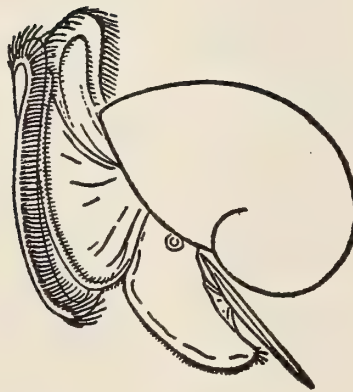
A generic characteristic is that the animal covers the canal and aperture with a thin shelly wall, leaving only the end of the canal open (GRAY, 1851). This is true of the species from the Gulf of California but with 2 significant exceptions. The shelly wall is never completely closed but provides access to the substrate through an irregular hole at the posterior end of the aperture. Also, there is a depression in the posterior wall, and sometimes a shallow canal, to provide for circulation of water.

The presence of an operculum in the genus has been questioned. The West Mexican specimens have a thin horny operculum similar to that of *Quoyula madreporarum* at all stages of growth.

The characteristics noted above have been observed in more than 30 specimens of dead and live-taken shells 6-36 mm in length including the canal. Until comparison with Indo-Pacific material can be made, it is best to cite the Gulf of California species as *Rhizochilus* sp. aff. *R. antipathus* Steenstrup, 1850.

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Avoidance of the Predatory Whelk *Lepsiella scobina albomarginata* by *Littorina cincta* and *Littorina unifasciata*

BY

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INTRODUCTION

THERE HAVE BEEN NUMEROUS ACCOUNTS of avoidance behavior shown by gastropod molluscs while in the presence of predators, especially sea stars (see reviews by BULLOCK, 1953; KOHN, 1961; FEDER & CHRISTENSEN, 1966; FEDER, 1972; UNDERWOOD, 1979). However, many of the experiments designed to observe these responses have only been performed in the laboratory, and the advantage of such behavior in the field can only be inferred (UNDERWOOD, 1979). I report on field experiments which demonstrate avoidance of the predatory whelk *Lepsiella scobina albomarginata* (Deshayes, 1839) by two species of *Littorina*.

Littorina cincta (Quoy & Gaimard, 1833) and *Littorina unifasciata* Philippi, 1847 are common between low HWS and high HWS on the rocky shore at Portobello, Otago Harbour, New Zealand (PILKINGTON, 1971). Whilst making daily counts of the numbers of gastropods in intertidal pools on a small rock platform close to Portobello Marine Laboratory, I observed, on three separate occasions, that pools which usually contained high numbers of *L. cincta* and *L. unifasciata* were devoid of all gastropods except for a single *Lepsiella scobina albomarginata*. MORTON & MILLER (1968) report that *L. scobina* (the "oyster borer" or "barnacle drill") preys upon oysters, mussels and barnacles, and has often been found drilling the last on the shore at Portobello (McKillup, unpublished, 1980). The lack of littorinids in pools visited by *L. scobina* suggests they may avoid this carnivore, and is investigated in the following experiments.

MATERIALS AND METHODS

Experiments were performed at low tide, in intertidal pools between low HWS and high HWS on the rocky shore near Portobello Marine Laboratory, in late October 1980. All took place on calm days, when little water was lost by evaporation from pools while snails were being observed, and during periods of high spring tides, so that pools had been refilled by the previous high tide.

RESPONSES TO PREDATORY AND NON-PREDATORY GASTROPODS

This experiment examined the responses of *Littorina cincta* and *Littorina unifasciata* to *Lepsiella scobina albomarginata* and the two herbivorous gastropods *Cellana ornata* (Dillwyn, 1817) and *Melagraphia aethiops* (Gmelin, 1791), all of which were present at the study site.

Twelve small pools, each having a surface area of approximately 40 cm², and which usually contained only the above mentioned littorinids, were numbered with fluorescent paint. The following 4 treatments, addition of either a similarly sized *L. scobina*, *C. ornata* or *M. aethiops* and a control wherein the pool was left undisturbed, were performed in each pool using a "blocked" design in time with 3 replicates of each treatment run daily for 4 consecutive days. Apart from the constraint that each occurred only once per pool, treatments were randomly assigned within the 4 blocks.

The numbers of *Littorina cincta* and *L. unifasciata* submerged in each pool were counted and gastropods used as treatments then added to appropriate pools. The latter took less than one minute to perform, thus treatments

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within each block were run virtually simultaneously. One hour later the numbers of submersed *L. cincta* and *L. unifasciata* in each pool were again counted, and gastropods used as treatments removed. Observations were also made of the behavior of both species of littorinids during this period.

RESPONSES TO SEAWATER CONTAINING SUBSTANCES EMANATING FROM PREDATORY AND NON-PREDATORY GASTROPODS

Observations made during the previous experiment suggested that littorinids were showing avoidance behavior without having contacted *Lepsiella scobina albomarginata*. Many molluscs respond to chemical substances emanating from predators (e.g., see PHILLIPS, 1975) and if this is so with *Littorina cincta* and *L. unifasciata*, they should display avoidance behavior in seawater which has previously contained *L. scobina*.

Six *Lepsiella scobina*, *Cellana ornata* and *Melagraphia aethiops* were collected from the shore and taken to the laboratory where each species was placed in a separate beaker containing 200 mL of seawater, while one contained no gastropods as a control. On the following day, gastropods were removed and all 4 beakers were taken to the study site. The design used in the previous experiment was repeated in the same pools, but with positions of treatments within each block re-randomized and 20 mL of appropriately treated seawater dripped into each pool, instead of adding gastropods or leaving pools undisturbed. As before, the numbers of submersed littorinids were recorded before and after treatments, and the behavior of snails also noted.

RESULTS

RESPONSES TO PREDATORY AND NON-PREDATORY GASTROPODS

Results appear in Table 1. It can be seen that the numbers of submersed *Littorina cincta* and *L. unifasciata* decreased significantly after the addition of *Lepsiella scobina albomarginata*, but none of the other 3 treatments had a significant effect (see results of one tailed Wilcoxon matched-pairs signed-ranks tests in Table 1). The behavior of snails was consistent with these results. Shortly after *L. scobina* had been added to a pool, all, or most *L. cincta* and *L. unifasciata* extended their tentacles and began moving rapidly until they were no longer submersed. Snails usually only moved upwards, unless within 1-2 cm of the

whelk, whereupon they moved away from it in any direction. In contrast, almost all of the littorinids in other treatments did not extend their tentacles, showed very little movement, and usually remained submersed, although pools were ringed with mixed clusters of emersed (i.e., individuals above the surface of the water) *L. cincta* and *L. unifasciata* and some exchange occurred between these and submersed snails, which is reflected in the data for treatments other than the addition of *L. scobina* in Table 1. Some emersed snails did descend into pools containing *L. scobina*, but invariably climbed out again within seconds of having become submersed. Furthermore, *L. cincta* and *L. unifasciata* were both observed contacting *Melagraphia aethiops* and *Cellana ornata*, but never *L. scobina*, even though they were far more active in the latter treatment.

RESPONSES TO SEAWATER CONTAINING SUBSTANCES EMANATING FROM PREDATORY AND NON-PREDATORY GASTROPODS

Results appear in Table 2, and confirm those from the previous experiment, in that only seawater in which *Lepsiella scobina albomarginata* had previously been kept caused a significant reduction in the numbers of both *Littorina cincta* and *L. unifasciata* submersed in pools (see results of one tailed Wilcoxon matched-pairs signed-ranks tests in Table 2).

The distribution of snails within some pools made it possible to drip seawater in the vicinity of isolated groups of *Littorina cincta* and *L. unifasciata*, and each species responded to seawater which had contained *Lepsiella scobina* by extending their tentacles and moving upwards until they were no longer submersed, but gave no response to "untainted" seawater, or that which had contained either *Cellana ornata* or *Melagraphia aethiops*.

As described previously, some movement of littorinids into and out of pools was observed in all treatments (see Table 2) but emersed snails descending into pools treated with seawater which had previously contained *Lepsiella scobina* again avoided becoming completely submersed.

DISCUSSION

There have only been three previous descriptions of avoidance behavior by littorinids. BULLOCK (1953) observed the responses of several gastropods to predatory and non-predatory sea stars and noted that *Littorina planaxis* Philippi and *Littorina scutulata* Gould "gave none of the abrupt or drastic signs of alarm so common in most of

Table 1

The numbers of (a) *Littorina cincta* and (b) *Littorina unifasciata* submersed in pools before, and one hour after the addition of *Cellana ornata*, *Melagraphia aethiops* and *Lepsiella scobina albomarginata*, plus a control where the pool was left undisturbed, together with values and probabilities for one tailed Wilcoxon matched-pairs signed ranks tests of significance for each treatment. *In cases where the number of positive and negative ranks are equal, both T values are presented.

N.S.: Not significant ($p > 0.05$).

Pool number	Treatments							
	Undisturbed		<i>Cellana ornata</i>		<i>Melagraphia aethiops</i>		<i>Lepsiella scobina</i>	
	Before	After	Before	After	Before	After	Before	After
(a) <i>Littorina cincta</i>								
1	24	24	26	29	16	16	18	9
2	31	42	21	21	22	33	39	9
3	2	1	2	0	3	2	24	0
4	3	3	23	23	2	3	12	0
5	12	18	32	27	21	21	38	11
6	2	3	1	1	6	5	21	0
7	5	8	1	3	8	4	6	2
8	15	15	8	8	3	3	8	1
9	2	2	6	4	2	3	3	1
10	8	5	5	5	5	12	13	2
11	31	34	51	47	53	54	62	16
12	7	5	13	18	9	9	16	2
Wilcoxon T	9.5		12.5		12.0		0	
probability	N.S.		N.S.		N.S.		< 0.01	
(b) <i>Littorina unifasciata</i>								
1	27	28	39	34	33	31	24	13
2	88	81	39	40	40	40	80	42
3	0	0	2	2	1	1	10	1
4	6	6	24	30	3	3	16	0
5	58	62	74	69	65	64	65	30
6	0	0	0	0	0	0	1	0
7	37	36	27	32	34	28	9	2
8	46	45	66	65	48	44	31	8
9	32	30	28	31	29	29	55	1
10	37	37	50	42	31	35	40	14
11	67	78	61	60	75	77	71	22
12	63	70	48	53	66	68	56	7
Wilcoxon T	21.5	14.5*	27.0	28.0*	11.5		0	
probability	N.S.		N.S.		N.S.		< 0.01	

the gastropods studied" but "did slowly crawl away from an isolated tube foot" of an unspecified predatory species, and concluded that these results "can be said to be positive since motionless snails were in most cases induced to crawl." Bullock does not give an account of the responses of *L. planaxis* or *L. scutulata* to non-predatory species and his methods and results are incompletely described, but a lack of response to the herbivorous *Patiria miniata* (Brandt) is implied later in the same paper. FEDER (1963) reported that if either of the predatory sea stars *Pisaster ochraceus*

(Brandt) or *Pycnopodia helianthoides* (Brandt) was placed in or allowed to drip into a tide pool, individuals of *Littorina scutulata* moved upwards until they were no longer submersed, but did not respond to seawater dripped into their pool. HADLOCK (1980) described how *Littorina littorea* (Linnaeus) responded to the juices from crushed conspecifics by "moving to sites in the pool where they were less visible to a human observer" and suggested that this response would reduce the probability of an individual being captured and eaten by the crab *Carcinus maenas*

Table 2

The numbers of (a) *Littorina cincta* and (b) *Littorina unifasciata* submersed in pools before, and one hour after the addition of 20 ml of seawater containing substances emanating from *Cellana ornata*, *Melagraphia aethiops*, and *Lepsiella scobina albomarginata* plus untainted seawater as a control, together with values and probabilities for one tailed Wilcoxon matched-pairs signed-ranks tests of significance for each treatment.

In the case where the number of positive and negative ranks is equal, both T values are presented.

N.S.: Not significant ($p > 0.05$).

Pool number	Treatments							
	Untainted		<i>Cellana ornata</i>		<i>Melagraphia aethiops</i>		<i>Lepsiella scobina</i>	
	Before	After	Before	After	Before	After	Before	After
(a) <i>Littorina cincta</i>								
1	12	12	21	22	23	26	25	1
2	27	33	23	23	8	08	13	4
3	3	3	1	0	1	0	0	0
4	1	1	2	2	0	2	5	0
5	33	31	37	40	46	42	38	12
6	2	1	2	2	9	9	1	0
7	10	12	7	7	4	4	4	1
8	9	15	7	7	12	11	3	4
9	3	3	4	4	5	5	6	0
10	11	6	9	8	3	3	15	0
11	36	35	44	49	54	55	45	0
12	11	9	10	9	14	15	10	2
Wilcoxon T		19.0	13.5	7.5*	12.0		0	
probability		N.S.		N.S.	N.S.		< 0.01	
(b) <i>Littorina unifasciata</i>								
1	12	12	37	42	43	43	26	1
2	36	34	27	29	20	21	31	15
3	1	1	1	1	0	0	1	1
4	11	13	15	16	7	8	11	1
5	68	64	69	66	69	70	63	13
6	0	0	0	0	0	0	0	0
7	18	18	17	21	4	6	14	5
8	30	31	22	17	39	40	34	21
9	28	28	27	27	28	30	23	1
10	24	25	17	20	21	21	22	1
11	31	35	65	62	79	76	63	1
12	33	42	37	37	48	48	53	14
Wilcoxon T		9.0		15.5		7.0		0
probability		N.S.		N.S.		N.S.		< 0.01

(Linnaeus). However, although Hadlock showed in the laboratory that snails placed in crevices were less vulnerable to predation by *C. maenas* than those on open rock, he did not show that the behavior elicited by the juices of other *L. littorea* actually decreased the probability of an individual being captured and eaten.

My experiments clearly demonstrate avoidance of *Lepsiella scobina albomarginata* by *Littorina cincta* and *L. unifasciata*. The responses of both species are elicited

at a distance by substances emanating from *L. scobina* and seem very similar to the behavior of *L. scutulata* described by FEDER (1963). The avoidance behavior of *L. cincta* and *L. unifasciata* is so effective that *L. scobina* was never observed contacting either species during experiments, and only ever found feeding upon sessile species (e.g., barnacles) on the shore. Assuming that capture by *L. scobina* will result in predation, moving upwards when near, and away in any direction when in very close proximity to

L. scobina will have an obvious selective advantage for an individual littorinid. At Portobello, both *L. cincta* and *L. unifasciata* occur between low HWS and high HWS, while *L. scobina* is most common around MTL but has been found higher on the shore than low HWS (McKillup, unpublished, 1980). The degree of overlap varies with location within New Zealand, but the distributions of both littorinids always extend higher on the shore than that of *L. scobina* (MORTON & MILLER, 1968). Therefore, moving upwards only when it is necessary to escape predation, in response to substances emanating from *L. scobina*, will enable both littorinids to coexist with this predator and thereby occupy and feed at lower levels on the shore than they could otherwise (see PHILLIPS, 1976).

SUMMARY

Observations made in the field at Portobello, Otago Harbour, New Zealand, suggested that the periwinkles *Littorina cincta* and *L. unifasciata* avoid the predatory whelk *Lepsiella scobina albomarginata*. This was confirmed in field experiments, and both littorinids were found to respond to water borne substances emanating from *L. scobina*.

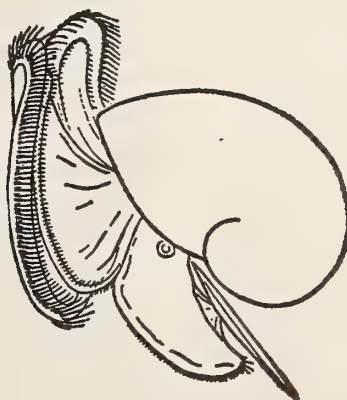
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Marine Laboratory. I thank Associate Professor J. B. Jillett for his interest and encouragement, and Dr. J. D. Roberts for commenting critically on an early draft of the manuscript.

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Acanthina punctulata

(Neogastropoda : Muricacea)

Its Distribution, Activity, Diet, and Predatory Behavior

BY

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(8 Text figures)

INTRODUCTION

Acanthina punctulata (Sowerby, 1825) is a predatory prosobranch gastropod common in the upper intertidal zone in the Monterey Bay area, California, at the northern limit of its known range. It resembles *Acanthina spirata* (Blainville, 1832), but probably represents a distinct species (McLEAN, 1969). Earlier work on both snails was reviewed briefly by ABBOTT & HADERLIE (1980). The main previous study of foraging in *Acanthina punctulata* by MENGE (1974), was carried out at Santa Cruz Island, off Southern California. The present study examines the intertidal distribution, diet, activity pattern, and predatory activity of this species. The function of the labial spine or tooth on the lip of the aperture of *Acanthina's* shell has long puzzled investigators. HEWATT (1934) gave a detailed account of its use to prevent closure of the operculum in barnacles, but other investigators have not confirmed this. This paper presents observations on the use of the spine in the predatory activity of *Acanthina punctulata*.

FIELD STUDIES OF DISTRIBUTION,
ACTIVITY PATTERN AND DIET

Studies were carried out on the north-eastern shore of Mussel Point, Pacific Grove, California, close to the Hopkins Marine Station of Stanford University, in the period May 1 to June 1, 1979. The study site was a relatively protected area, 20 by 15 m, accessible at high tide. Bare rocks and rocks bearing barnacles were prevalent in the study

site; tidepools, shaded crevices, and beds of the sea anemone *Anthopleura elegantissima* (Brandt, 1835) also existed amongst these rocks. Vertical position of animals in the intertidal zone was established using a surveyed benchmark near the study site.

METHODS

To study the distribution of *Acanthina punctulata* on various substrata, 50 quadrats, each 1 m², were selected in the study area at coordinates picked by use of a random number generator. Within each quadrat the percent of the total area represented by each type of substrate was approximated using measurements obtained with a meter stick to an accuracy of about $\pm 5\%$; data for the 50 quadrats were then averaged to yield the percent of each type of substratum for the total area.

For a study of activity, 60 *Acanthina punctulata* in the 20 x 15 m study site were selected, using a random number coordinate point method. They were marked with red fingernail polish and followed over a 25 hour tidal cycle. Observations were made every 2 hours of movement, feeding, and condition of emersion of each snail. A snail was classified as moving if over a 30 second period it could be seen crawling with its tentacles extended. With regard to condition of emersion, animals were classified as dry (totally exposed above water), awash (partially submerged or alternately exposed and submerged), or submerged (totally under water). At low tide, numerous *Acanthina* were found in *Anthopleura elegantissima* beds, or submerged in tidepools. A snail in a tidepool or anemone bed that was being washed by the incoming tide was still counted as being in a tidepool or anemone bed.

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When a snail was seen feeding, a circle of 10 cm radius was placed around it and the relative abundance of different prey available was subjectively determined on a scale of 0 to 4 (0 = none, 4 = very abundant). In determining feeding activity, I did not distinguish between drilling and eating. An *Acanthina* on a prey species (e.g., another snail), with a drill hole just beneath it, was counted as feeding. When the prey consisted of barnacles, (e.g., *Chthamalus* spp., *Balanus glandula*), feeding activity was harder to determine. If a snail was poised over one barnacle and looked as though it could be feeding, I carefully lifted up the anterior portion of the snail and looked below. Often I could see the proboscis extending into the barnacle. If the proboscis was not visible, yet the barnacle underneath was gaping open, I counted the snail as feeding. When any uncertainty existed, the snails were counted as not feeding. If the snail was feeding, the prey was marked with a small dot of fingernail polish so that if the snail was seen feeding there at a later time I could tell whether it was feeding on old or newly caught prey. Supplementary observations on feeding and movement were obtained at eight high tides and eight low tides.

RESULTS AND DISCUSSION

The results of the distribution studies are shown in Figures 1 and 2. In vertical distribution at low tide (Figure 1), the snails occurred 60 cm to 1.5 m above mean lower low water (MLLW), with the majority at 75 m to 1.2 m in a zone including some of the red algae *Gigartina papillata* (C. Agardh) J. Agardh (1848) and *Endocladia muricata* (Postels & Ruprecht) J. Agardh (1847). The snails at the 60 cm level were in and around tidepools; those at 1.5 m were on rocks bearing small but scattered barnacles.

Figure 2 shows the distribution of *Acanthina punctulata* on different substrata in 50 square meters of the study site. Nearly half the substratum consisted of bare rock or rock bearing *Chthamalus* or *Balanus*, and 37% of the *Acanthina* occurred here at low tide. The sandy bottoms of tidepools accounted for approximately 23% of the area sampled, and contained 30% of the *Acanthina* present. *Anthopleura elegantissima* beds accounted for only 3% of the area sampled, but contained about 20% of the *Acanthina* at low tide.

Figure 3 shows the activity of the *Acanthina* population over a 25 hour tidal cycle. Under conditions of low tide, many snails are exposed and dry; as the tide rises, they are wetted. Snails which are in the moist environments of *Anthopleura elegantissima* beds and tidepools at low tide crawl up onto rocks and barnacles now washed or covered

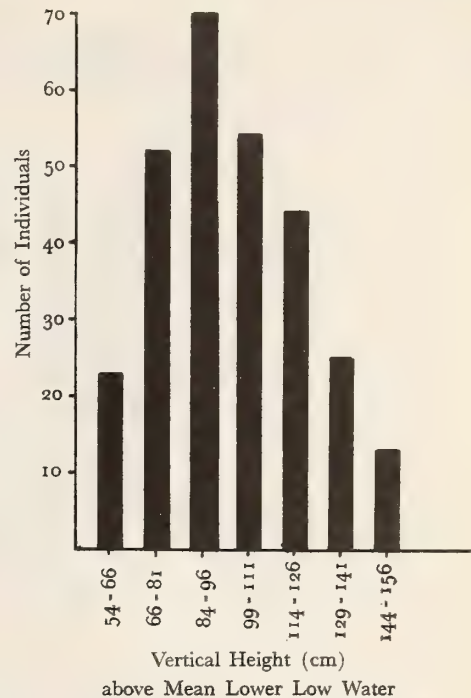


Figure 1

Vertical distribution of the population of *Acanthina punctulata* in a 15×20 m rectangular study area at Mussel Point, Pacific Grove, California

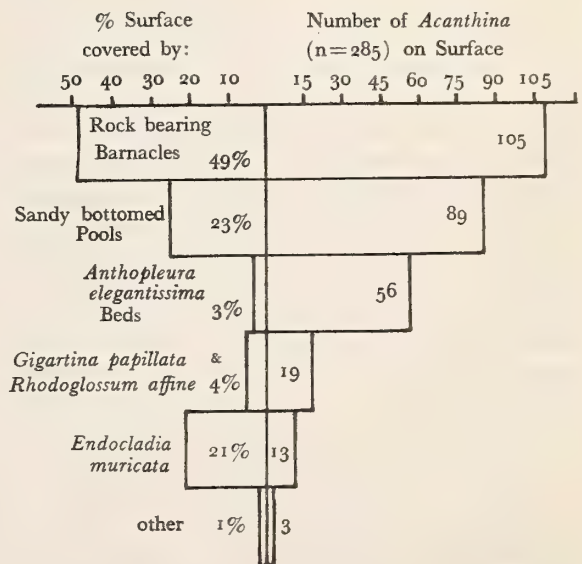


Figure 2

Distribution of the population of *Acanthina punctulata* on different types of surfaces in 50 m² at the study site

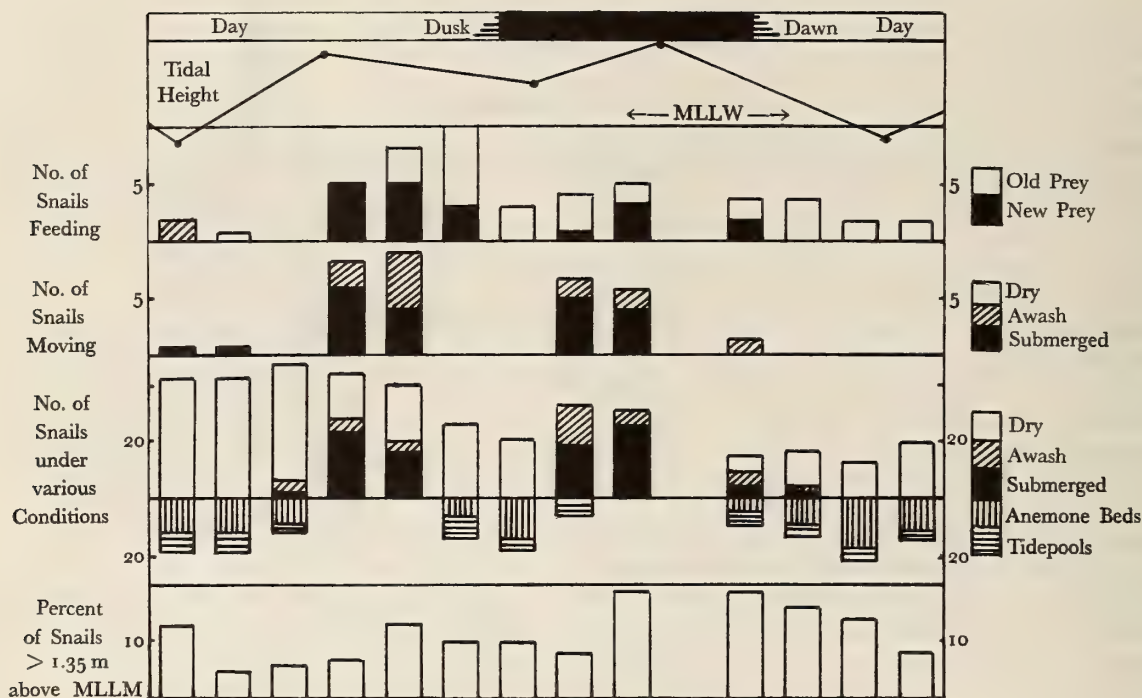


Figure 3

Movement and feeding of 60 *Acanthina punctulata* over a 25 hour tidal cycle

by the incoming tide. As the tide rises, the number of snails on rocks and barnacles 1.35 m or more above mean lower low water also rises, and then decreases again as the tide goes down. At low tide when most snails are exposed to air there is little movement; those snails moving during periods of low tide are almost all awash or submerged. As the tide rises and more snails are wetted the number moving increases. Feeding follows the same pattern, increasing as the tide rises, and decreasing as it falls. Most snails found feeding at low tide are consuming prey located during the previous high tide. That hunting occurs at high tide is confirmed by data on the number of new prey caught as a function of tidal height during the 25 hour study (Figure 4); the number of new prey caught increases significantly (least-squares regression, $p < 0.01$) as the water level rises. Supplementary data on feeding and movement (Figure 5) also show more movement and feeding at high tide than at low tide; of the snails moving and feeding, most were either awash or submerged.

The pattern of activity noted above confirms the obser-

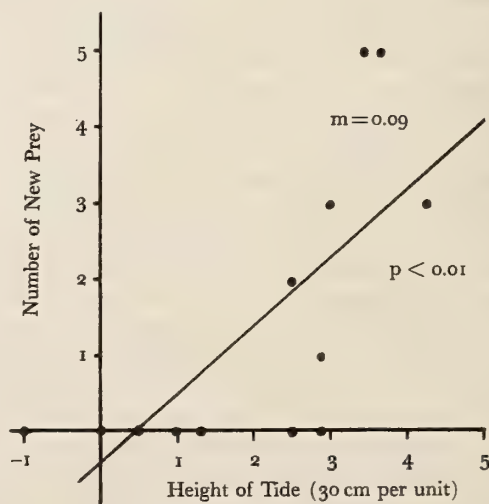


Figure 4

Relation of number of new prey caught by *Acanthina punctulata* to tidal height over a 25 hour period

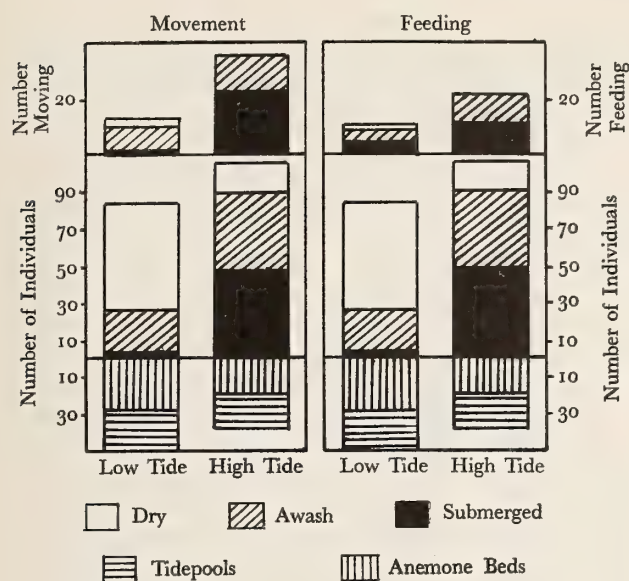


Figure 5

Summary of field observations during 8 high and 8 low tides. Lower portions of the graph indicate the number of individuals of *Acanthina punctulata* observed for high and low tides, and the condition of emersion or exposure. Top portions of the graph show the number of these individuals moving or feeding for a given condition of the tide

vations of GLYNN (1965) that at high water more *Acanthina* move up into the *Endocladia-Balanus* belt and commence to feed. MENGE (1974), in her study on the prey selection and foraging activity of *Acanthina punctulata* at Santa Cruz Island, found that the population there forages at low tide but sometimes continues to feed over the high tide. It seems possible this difference may be related to differences in the physical nature of the study sites; if Menge's site experienced more wave action than my protected locality, this might have restricted foraging at high tide.

Figure 6 shows the diet of the *Acanthina* population in relation to the relative abundance of the prey. The abundant barnacles *Chthamalus* spp. and *Balanus glandula* (Darwin, 1854), were consumed most frequently. Unlike the Santa Cruz Island population reported by MENGE (1974), many *Acanthina* at Pacific Grove were found feeding on *Tegula funebris* (A. Adams, 1885) which is abundant here. Most *Tegula* were captured near tidepools. Two smaller gastropods, *Littorina scutulata*

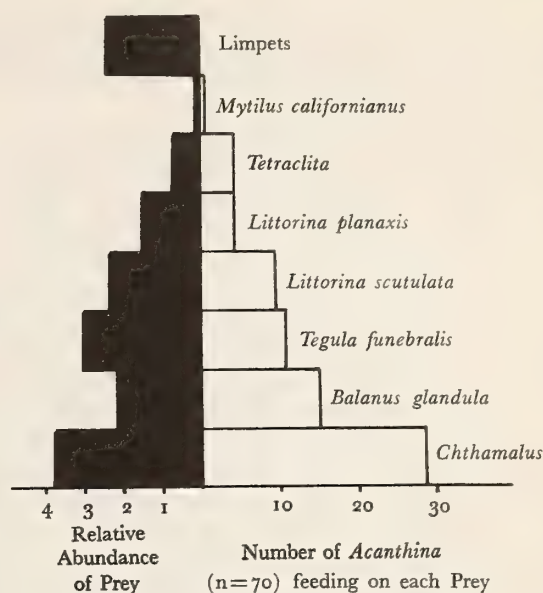


Figure 6

Feeding preferences of 70 *Acanthina punctulata* found feeding in the field at the Mussel Point study site. Relative abundance of prey species were subjectively determined on a scale of 0 to 4 (0 = none; 4 = very abundant)

(Gould, 1849) and *Littorina planaxis* (Philippi, 1847), were also consumed readily in the field. *Littorina planaxis* normally exists in a zone above the *Acanthina* population; usually the individuals preyed upon are those knocked down by wave action into the zone of *Acanthina*. *Collisella digitalis* (Rathke, 1833), and *Collisella scabra* (Gould, 1846) were both very abundant in the study area but none were observed being eaten. *Acanthina* in laboratory aquaria showed the same general preferences as in the field, but in the laboratory selected a wider variety of prey items including the stalked barnacle *Pollicipes polymerus* (Sowerby, 1883), the limpets *Collisella digitalis* and *Collisella scabra*, and the bivalve *Mytilus californianus* (Conrad, 1837).

PREDATORY BEHAVIOR

When observed in the laboratory, *Acanthina punctulata* approaches potential prey with cephalic tentacles extended, swinging its shell to the left and right on its vertical

axis as it moves along. The orientation of the shell often places the marginal spine directly in front of the snail, and cephalic tentacles can often be seen extending out on either side of the spine.

Acanthina usually first contacts its prey with its tentacles. If the prey is a snail the predator then places the anterior portion of its foot upon the prey and starts to mount it. This behavior was also noted by BIGLER (1964) and MENGE (1974). Once the prey is positioned underneath the foot of the *Acanthina*, drilling commences. Drilling involves a secretion from the accessory boring organ (ABO) located in the propodium, which softens the shell of the prey; drilling then involves rasping by the radula of the softened portion of the prey's shell (HEMINGWAY, 1973). Most snail prey are drilled at the same place, the thickest part of the shell just external to the point of attachment to the columellar muscle, as noted by Menge (1974). In my studies, consumption of an individual snail took from 2 hours to a day depending on the size of the prey. Observations of *Acanthina* feeding on meat removed from *Littorina planaxis* and placed in a deep glass vial provided a good view of the extended proboscis. Meat is detached from the prey in relatively large chunks and passed rapidly along the esophagus.

Special efforts were made to observe the use of the marginal spine of *Acanthina punctulata*. PAINE (1966) who studied several species of *Acanthina*, observed no use for the spine except perhaps as a brace or wedge when drilling prey. I have often seen the spine wedged against the inside edge of the prey's operculum while *Acanthina* drilled the shell of another snail. HEWATT (1934) describes another use of the spine in preying on barnacles. He says, "When attacking a barnacle, the snail assumes a position above the opening of the barnacle shell so that this spine is directly above the line of contact of the closed scutes of the barnacle. The *Acanthina* usually takes this position when the tide is out and the barnacle thus is closed. When the water returns over the area, the natural reaction of the barnacle is to open up and begin the feeding activities. As soon as this occurs, the snail quickly inserts its spine into the opening between the scutes, the proboscis is everted, and the soft parts of the barnacle are consumed." MACGINITIE & MACGINITIE (1968) repeat this general observation.

In the present study I observed the use of the spine on a barnacle four times, twice in the laboratory and twice in the field. Both times in the field the action occurred when the snails were awash on an incoming tide. On one occasion, the *Acanthina* crawled upon a *Chthamalus* and

sat there for a minute or so with no apparent motion. Then the *Acanthina* raised the anterior portion of its shell (its foot still firmly on the side of the barnacle) and, in a hammering motion, brought it down on top of the opercular scutes of the barnacle. It then lifted its shell and repeated the same motion, this time remaining with the spine over the operculum for approximately 2 minutes. I was not able to see whether or not the spine was actually separating the scutes and entering the mantle cavity of the barnacle. After this period, the snail raised its spine and settled over the prey in a feeding position. After 15 minutes I tipped up the predator's shell to reveal the proboscis everted into the barnacle's opercular opening. When the *Acanthina* was removed, the barnacle remained gaping open as if paralyzed.

The same general behavior was observed in the laboratory. However, when one *Acanthina* lifted its shell up and gave the hammering blow with its spine, it thrust the spine between the wall plates and the opercular plates of the barnacle. It repeated this motion twice (the first time, the spine did not reach the opercular opening, but slid down the side of the barnacle). The snail stayed in this position for 2.5 minutes, and then took its spine out and settled over the barnacle as if to feed. At this point, I lifted the snail off; the barnacle was not gaping, and it gave a fast closing response when touched with a probe. After 45 minutes the barnacle still showed no signs of gaping. I replaced the snail near the barnacle. Almost immediately it moved over the barnacle in a feeding position, the anterior portion of the snail directly over the opercular plates of the barnacle. After a few minutes, I lifted the snail off the barnacle again; I could see its proboscis slowly retract from the gaping opercular plates. When the gaping barnacle was touched with a probe, the operculum closed slowly but not totally. I could see no damage to the plates and there was no bore hole present.

These observations suggest the hypothesis that, when preying upon barnacles, *Acanthina punctulata* uses a fast-acting toxin, and that the spine helps the predator to inject or apply this toxin into the mantle cavity of the barnacle, causing paralysis.

Toxic choline esters have previously been reported from the hypobranchial gland of *Acanthina spirata* (see BENDER, *et al.*, 1974; the species used in the study was almost certainly *Acanthina punctulata* (D. P. Abbott, pers. comm.)). In the present work, laboratory studies were conducted to test the hypothesis that *Acanthina punctulata* uses secretions from its hypobranchial gland to paralyze barnacles.

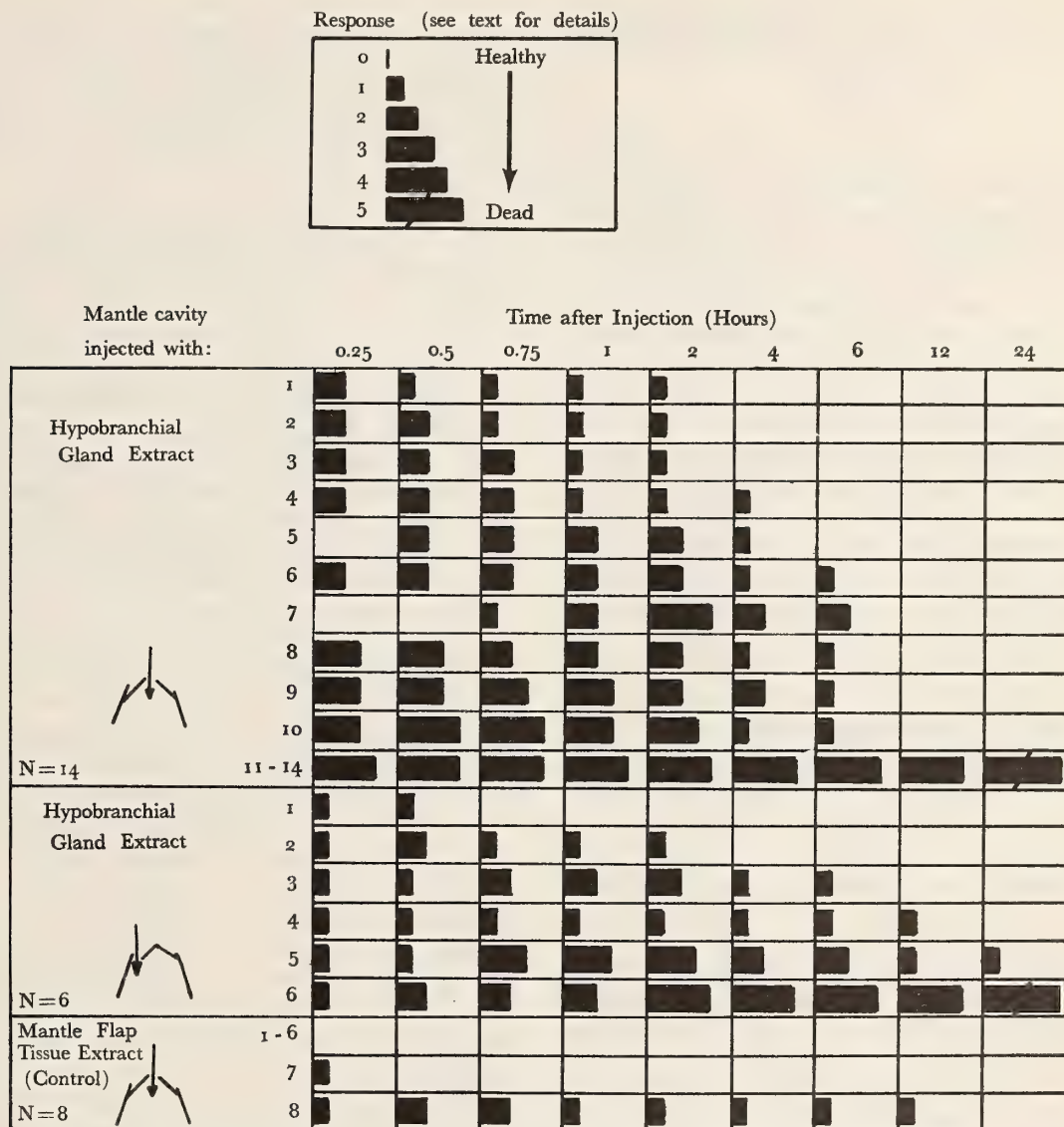


Figure 7

Responses of *Chthamalus dalli* to 0.2 mL injections of hypobranchial gland or control extract from *Acanthina*. Hypobranchial extract injections were given through the opercular openings in 14 barnacles and in the soft tissue between the operculum and wall plates in 6 barnacles. The responses of the barnacles to probing observed at specified intervals over a period of 24 hours were graded on a

scale of 0 to 5 (0 = full healthy response - plates close and clamp down; 1 = tight closure of opercular scutes but no clamping down; 2 = closure of operculum slow, or plates do not close tightly; 3 = very slow closure, or no closure; 4 = no response at all to probing; 5 = death, determined after 24 hours of no response). Barnacles showing identical responses (experimental individuals 11-14, control individuals 1-6) are grouped on single lines

TOXIC EFFECTS OF HYPOBRANCHIAL GLAND EXTRACTS

METHODS

Fresh *Acanthina punctulata* and rocks or shells bearing undamaged barnacles (*Chthamalus* spp.) were gathered from the field before each experiment. To test the response of *Chthamalus* to two known choline esters, benzoyl chloride and conbachol, a solution of 1 mg of choline ester per 1 mL of sea water was injected; plain sea water was used in controls. Hypobranchial gland extracts used consisted of four hypobranchial glands macerated in 50 mL of sea water. A whitish-green mucus was often secreted from the hypobranchial gland during dissections; this was added to the gland extracts. Control extracts consisted of other tissue from the roof of the mantle cavity, in approximately the same mass as four hypobranchial glands, ground up in 50 mL of sea water. Injections of 0.2 mL of extract into the mantle cavity were made with a fine needle and a 1 mL syringe. For injections through the opercular aperture, I waited until the barnacles opened to feed and then gently inserted the needle into the mantle cavity. For injections at the side of the operculum, I injected through the soft tissue lying between the opercular plates and the wall plates of the barnacles. After injection, animals were probed at intervals and their responses recorded on a graded scale (see Figure 7 and legend).

RESULTS AND DISCUSSION

When 14 barnacles were injected through the opercular opening with solutions of known choline esters, paralysis occurred within 1 to 5 minutes, after which the barnacles responded slowly or not at all to probing. Control barnacles, injected with sea water through the opercular plates, showed no paralysis.

When a sea water solution of hypobranchial gland extract was injected through the opercular plates of barnacles, a paralyzing response was observed much like that noted for the injections of choline esters. The results are summarized in Figure 7. All experimental animals showed some degree of paralysis, but most recovered and showed normal responses in 6-8 hours. Only one of the eight control barnacles showed a diminished response.

These results strongly suggest that *Acanthina punctulata* uses a toxic secretion, probably from the hypobranchial gland, to paralyze the barnacles it preys upon. Use of a toxin from the salivary glands is not excluded, but preliminary tests with salivary gland extracts showed no toxic

effects on barnacles. Laboratory and field observations in general support the hypothesis that poison, rather than physical force, is used to gain entry to barnacles; usually when a feeding *Acanthina* is removed from a gaping barnacle, no bore holes or other indications of physical damage could be seen around the opercular plates.

REMOVAL OF SHELL SPINE: EFFECTS ON BARNACLE PREDATION

It appears *Acanthina* makes use of the spine on its shell in applying the toxin when preying on barnacles. To provide further information on this, 10 *Acanthina* with normal spines were placed in an aquarium with rocks bearing *Chthamalus* spp., while 10 other *Acanthina* of similar size but with the spines filed off were placed in a second aquarium similarly provided with rocks bearing *Chthamalus*. All *Chthamalus* were carefully inspected at the start of the experiments, and only healthy animals were used. The experiment was repeated three times, the snails being left to feed on the barnacles for periods of 5, 7, and 10 days respectively in the three trials. At the end of each test the condition of all barnacles in both aquaria was determined and ranged under four categories: healthy; shell empty, no damage to opercular plates; shell empty, with opercular plates present but somewhat damaged (scraped, broken, etc.); shell empty, with opercular plates gone. Pooled results of the three trials are shown in Figure 8.

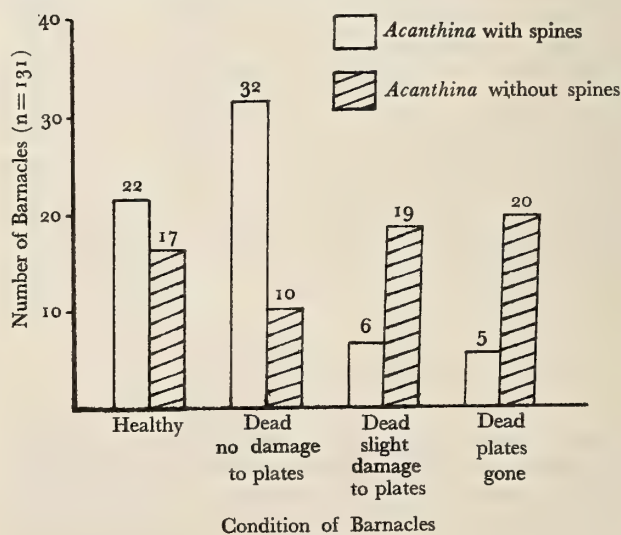


Figure 8

Results showing the damage inflicted on *Chthamalus dalli* by normal *Acanthina punctulata* and by snails with spines filed off

Confronted with a similar food supply, *Acanthina* with and without spines eat about the same number of barnacles. However, snails without spines generally inflict more damage to barnacles than snails with spines, and three times as many of the barnacles fed upon by spineless *Acanthina* have their opercular plates completely ripped off in the feeding process than in the case of *Acanthina* with normal spines. When the *Acanthina* with normal spines did inflict great damage to the opercular plates, the barnacles being preyed upon seemed to be in an awkward position for the snails. For instance, in one trial involving *Acanthina* with normal spines, four barnacles were clustered together. Two of these barnacles were large and easily accessible while the other two were smaller and lay in a crevice between the larger two, making them difficult for the snails to reach. After a week, the two larger barnacles were dead and eaten but the shells appeared undamaged; opercular plates were present and not broken. The smaller more inaccessible barnacles had the opercular plates completely ripped off.

GENERAL DISCUSSION

The observations and experiments performed support the idea that the spine of the *Acanthina* is used in a way that allows the snail to prey on barnacles without resorting to force or drilling to breach the operculum.

The anatomy of *Acanthina* permits some speculations as to how the spine might be related to the poison secreted by the hypobranchial gland. Near the siphon on the lip of the mantle fold is a slightly protruding tongue of tissue corresponding in position to the spine. This slight protrusion is located near the anterior end of the hypobranchial gland. Although carefully looked for, no special ciliary tract was found connecting the hypobranchial gland with the spine area; it is possible that a hypobranchial gland secretion could flow along the roof of the mantle cavity on the inside and drip out near the spine. The spine might be used to pry open or to hold open the scutes of the barnacle as poison is dripped in, or the spine and corresponding small extension of the mantle margin might be used as an applicator, applying the toxin to the soft tissues or to the operculum opening of the barnacle.

The barnacles *Chthamalus* spp. and *Balanus glandula* provide relatively small amounts of food to a predator. From this point of view, it would seem desirable for *Acanthina* to have developed a relatively fast and efficient alternative to drilling as a means for opening barnacles. The absence of drill marks, the obvious paralysis of the prey, and the experiments performed, all suggest that

Acanthina does have such a means, and that it involves the hypobranchial gland and the spine.

SUMMARY

1) *Acanthina punctulata* on the rocky shore at Pacific Grove, California, occupies a vertical range 60 cm to 1.5 m above mean lower low water, with the majority of snails in the 75 cm to 1.2 m zone. Here *Acanthina punctulata* is most commonly found on rocks bearing barnacles, in sandy bottomed tidepools, and in beds of the sea anemone *Anthopleura elegantissima*.

2) Activity and feeding of *Acanthina punctulata* at Mussel Point vary mainly with the tidal cycle. As the tide ebbs, many *Acanthina* retreat to wet situations in tidepools and *Anthopleura* beds, while others remain relatively motionless on exposed rock surfaces. As the tide rises, activity increases and more snails crawl up the rocks now washed or covered by the sea. The number of snails seen feeding rises and falls with the tide. Most snails feeding at low tide are eating prey caught during the previous high tide.

3) The diet of *Acanthina punctulata* at Pacific Grove includes the barnacles *Chthamalus* spp. and *Balanus glandula*, and the gastropods *Littorina planaxis*, *Littorina scutulata*, and *Tegula funebris*.

4) Both field and laboratory observations on *Acanthina punctulata* indicate a hammering action of its spine on the opercular opening of barnacle prey. Barnacles exhibit partial paralysis within 15 minutes of this hammering, permitting easy entry of the predator's proboscis. The paralysis of the barnacle coupled with the absence of drill marks or other damage on the opercular plates suggests that the snail deposits a toxin on the barnacle's operculum. Hypobranchial gland extract from *Acanthina* is demonstrated to have this same paralyzing affect when injected into the mantle cavity or the soft tissues at the margin of the operculum of *Chthamalus dalli*. The spine may be used to pry open or to hold open the scutes of the barnacle as secretions from the hypobranchial gland drip in, or it may be used, perhaps along with the edge of the mantle flap as an applicator, to apply the toxin to the soft tissues or to the opercular opening of the barnacle.

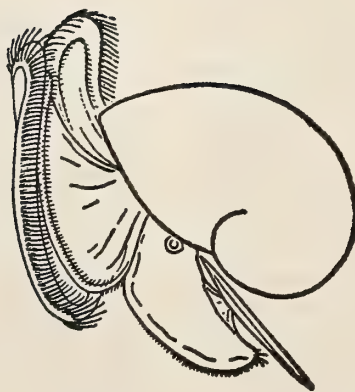
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Evidence of Gregarious Settlement in the Larvae of the Marine Snail *Collisella strigatella* (Carpenter)

BY

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INTRODUCTION

THE LARVAE OF MANY INVERTEBRATES settle selectively on substrates with particular physical or biological characteristics (THORSON, 1964; MEADOWS & CAMPBELL, 1972; CRISP, 1974, 1976, 1979; SCHELTEMA, 1974). The tendency of some larvae to settle in response to the presence of individuals of their own species is called "gregarious settlement" (CRISP, 1974). Gregarious settlement has been documented by means of field or laboratory experiments for several species of sessile marine invertebrates: a bivalve mollusc (COLE & KNIGHT-JONES, 1949), barnacles (KNIGHT-JONES & STEVENSON, 1950; KNIGHT-JONES, 1953a), polychaetes (KNIGHT-JONES, 1951, 1953b; WILSON, 1968; STRAUGHAN, 1972), a bryozoan (WISELY, 1958), a hermatypic coral (LEWIS, 1974), and a tunicate (YOUNG & BRAITHWAITE, 1980).

There apparently have been few studies of this phenomenon in mobile species. I know of only one case in which gregarious settlement in a mobile species was experimentally demonstrated. KISELEVA (1967) studied two species of gastropods, *Rissoa splendida* Eichwald and *Bittium reticulatum* (da Costa), which live on algae, particularly of the genus *Cystoseira* C. Agardh. In her laboratory experiments both snails settled preferentially on algae (mostly *Cystoseira*) and near young of their own species. In other experiments she showed that the larvae recognized both the algal substrate and other individuals of their own species by means of a chemotactile sense.

Here I present evidence which suggests that larvae of the intertidal limpet, *Collisella strigatella* (Carpenter, 1864), also recognize and selectively settle near adults of their own species.

METHODS

Collisella strigatella is one of several species of acmaeid limpets which live on hard substrates in the intertidal zone along the California coast. In the vicinity of Santa Barbara its local distribution overlaps those of three other abundant species: *Collisella digitalis* (Rathke, 1833), *Collisella scabra* (Gould, 1846), and *Notoacmea fenestrata* (Reeve, 1855). All these species graze the thin film of diatoms and juvenile stages of macroalgae which cover intertidal rocks. In the lower and middle intertidal zones, *C. strigatella* and *N. fenestrata* are the most abundant limpets on boulders less than about 50 cm high which have much open space (DIXON, 1978).

I censused limpets in boulder fields at Arroyo Hondo about 50 km west of Santa Barbara, and at Toro Canyon, about 8 km east of Santa Barbara. At these locations the boulders are set in sand and migration is generally not possible. I estimated the areas of boulders by dividing them into regular plane figures with chalk, measuring the appropriate dimensions, calculating the areas, and summing them. Based on observed changes in size frequency distributions with time, *Collisella strigatella* less than 6 mm in shell length probably settled within about 4 months of the census. I treated these as recently settled young and larger animals as representing cohorts from previous settlement seasons and did a correlation analysis of the densities of the two size classes. For this analysis I used data from those sampling periods when recently settled young were most numerous.

At Arroyo Hondo I fenced square areas, 15 cm on a side, with plastic mesh (VEXAR, Dupont Corp.) on a large, flat rock located about +0.15 m (+0.5 ft) in the

intertidal zone. The fenced area was covered with the typical film of diatoms and patches of crustose corallines. There was no apparent difference among fenced plots and treatments were completely randomized among plots. Within each fenced plot, I confined 10 limpets in the following species combinations: 10 *Collisella strigatella* alone; 5 *C. strigatella* with 5 *Notoacmea fenestrata*; or, 10 *N. fenestrata* alone. There were 4 replicates of each treatment. All the adults were about the same shell length (*C. strigatella*: \bar{X} = 10.1 mm; *N. fenestrata*: \bar{X} = 10.8 mm). In October 1976 there were many newly settled limpets within the fenced plots. All were less than 4 mm in shell length and many were around 2 mm long. All the animals which were large enough to identify to species were *C. strigatella*. The smallest individuals were either *C. strigatella* or *N. fenestrata*, but were not distinguishable in the field even with the use of a hand lens. However, they were distributed among treatments in the same proportions as the identifiable recruits and the following observations indicate that they were also *C. strigatella*: 1) *N. fenestrata* generally settle earlier in the year (FRITCHMAN, 1961; DIXON, 1978); 2) On 34 boulders in the same area as the experimental boulder there were 45 *C. strigatella* less than 4 mm long but only 3 *N. fenestrata*, and; 3) Based on growth rate data (Dixon, unpublished), *N. fenestrata* that were about 2 mm long in October would have been large enough to identify in November but still in the 0-4 mm size class, or perhaps the 4-8 mm class. However, on 29 boulders censused in November there were no *N. fenestrata* less than 4 mm long and only 5 between 4 and 8 mm. Therefore, I included all the new recruits in the experimental plots in the analysis and compared the three treatment means using a one-way analysis of variance and a least significant difference test for *a posteriori*, pair-wise comparisons.

RESULTS AND DISCUSSION

Within boulder fields the density of small, recently settled *Collisella strigatella* on boulders isolated in sand is positively correlated with that of older individuals (Table 1). Since the sand prevents migration, this pattern must result from events taking place at the time of settlement or shortly thereafter. In the absence of migration, and given constancy in the suitability of habitat, a correlation between the density of adults and young is necessary, though not sufficient, evidence of gregarious settlement. The pattern could also be caused by mortality of recently settled larvae in unsuitable habitats, or by selective settlement in response to other biological or physical characteristics of boulders to which the adults had also responded.

The results of the experiment involving fenced adults suggests that the larvae respond to conspecific adults. The analysis indicates that newly settled *Collisella strigatella* occurred in greater numbers in those fenced plots that contained adults of the same species than in plots which contained only adults of the related species, *Notoacmea fenestrata* (Table 2). The only difference between these plots was the species composition of the adults. Nevertheless, since the larvae were not observed at the time of settlement, the results can be interpreted in several ways: 1) the larvae settled randomly with respect to the adults of the two species but suffered greater mortality in plots containing only *N. fenestrata*; 2) the larvae settled randomly with respect to the adults of the two species but dispersed out of the plots containing only *N. fenestrata*, or; 3) the larvae recognized and selectively settled near adults of their own species. The first hypothesis can be rejected on the basis of the experimental results—recruits were as numerous in plots in which half the adults were

Table 1

Correlation between the density of small and large limpets, *Collisella strigatella*, in two southern California boulder fields. The small limpets were all less than 6 mm in shell length and probably had settled within about four months of the census.

Location	Date of census	Number of boulders censused	r	P
Arroyo Hondo	07/10/76	30	+ 0.37	< 0.05
Arroyo Hondo	07/03/77	57	+ 0.48	< 0.01
Arroyo Hondo	11/14/77	48	+ 0.45	< 0.01
Toro Canyon	12/12/77	42	+ 0.34	< 0.05

Table 2

Effect of the presence of previously settled individuals of the same and of a related species on the recruitment of *Collisella strigatella*. Limpets (ca. 10 mm shell length) were confined in fenced plots in three species combinations:

10 *C. strigatella* alone; 5 *C. strigatella* with 5 *Notoacmea fenestrata*, and; 10 *N. fenestrata* alone.

After a settlement episode the number of recently settled *C. strigatella* in each plot was counted.

The lines connect means which are not significantly different by a Least Significant Difference test ($\alpha = 0.05$).

Treatment		Mean number of recruits			
5 <i>C. strigatella</i> and 5 <i>N. fenestrata</i>		12			
10 <i>C. strigatella</i>		10			
10 <i>N. fenestrata</i>		4			
Analysis of variance					
Source of variation	DF	SS	MS	F	P
Treatment	2	158	79.0	37.6	< 0.001
Error	9	19	2.1		
Total	11	177			

N. fenestrata as in plots in which the latter were absent. That the results could be due to selective migration soon after settlement cannot be rigorously ruled out since it was probably possible for very small limpets to move through the fences. However, since newly settled individuals were abundant in the mixed species plots, they were apparently not reacting negatively to the presence of *N. fenestrata*. On the other hand, adults of both species were present on the unfenced portions of the rock and the new recruits may have sought out conspecific adults outside the plots. Although this is a possibility, I think the fences would have been a serious barrier to migration. The interpretation of the experimental results that I find most compelling is the third: *Collisella strigatella* recognize and selectively settle near individuals of their own species.

Although the results of both censuses of islands of habitat and the field experiment suggest gregarious settlement, this remains a hypothesis to be tested further. The definitive test must await the successful culturing of these larvae since it requires exposing competent larvae to appropriate substrates in the presence of adults of the same and of different species (cf. KISELEVA, 1967; CAMERON & SCHROETER, 1980).

If *Collisella strigatella* settle gregariously, one wonders why the correlation between the density of adults and newly settled individuals is not higher. It is probably because the habitat on a given boulder often changes significantly in a relatively short time. For example, barnacles settle and grow on boulders where they were previously absent, or disappear from rocks on which they were once

abundant. As a result, a boulder may be a more or a less suitable habitat during a given settlement episode than when the adults settled (CHOAT, 1977; DIXON, 1978). Despite this phenomenon, gregarious settlement could aid species like *C. strigatella* in the selection of a suitable habitat because of the tremendous variability in environmental conditions within the intertidal zone. Even physically identical boulders are very different habitats when located at different tidal heights. Limpets which settle on boulders high on the shore are subject to severe physiological stress from drying conditions. Those which settle on boulders in the low intertidal are at a greater risk of being eaten by sea stars or having space preempted by sessile species (DIXON, 1978). Within a given tidal zone there are also significant, and less predictable, variations in environmental conditions. For example, some areas are much more subject to seasonal influxes of sand. In those areas boulders may periodically be completely buried whereas similar boulders 30 m away will remain uncovered. For animals like limpets which live on islands of substrate that occur over a greater range of environmental conditions than is suitable for the species, the presence of conspecific adults is probably one of the best indications of a congenial habitat.

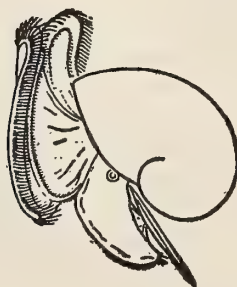
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Fusitriton oregonensis from the Patton Seamount in the Gulf of Alaska

BY

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(2 Text figures)

IN JUNE, 1979, six live specimens of *Fusitriton oregonensis* (Redfield, 1848) were caught in sablefish (*Anoplopoma fimbria*) and king crab (*Paralithodes camtschatica*) traps during exploratory fishing operations conducted by the National Marine Fisheries Service on the Gulf of Alaska seamounts. Although *F. oregonensis* has been found on a seamount before (BIRKELAND, 1971), these specimens are, I believe, the first record of this species from a seamount in the Gulf of Alaska.

The Patton seamount was the only seamount, of the eight sampled, where *Fusitriton oregonensis* was caught. The absence of *F. oregonensis* on the other seamounts may be due to their greater depth (Figure 1) because all seamounts except Patton were deeper than the reported maximum depth (433 m) of *F. oregonensis* in the Gulf of Alaska (SMITH, 1970). One of the Patton seamount specimens, however, was collected at 540 m, 107 m deeper than the previous record.

The Gulf of Alaska seamounts are isolated from adjacent areas of comparable depth along the continental slope by depths exceeding 3 000 meters. Although our sampling was not exhaustive, *Fusitriton oregonensis* was the only snail obtained on our survey and may well be the only shallow water snail to have colonized the seamounts. Undoubtedly, the reason for this is that *F. oregonensis* has a pelagic larva (SMITH, 1970), a feature which is unusual for a snail inhabiting such high latitudes (A. Kohn, pers. comm.). Unlike the Emperor seamounts, where an endemic species of *Fusitriton* has evolved (HABE, 1979), the Patton seamount is not completely isolated and apparently receives at least sporadic recruitment of larvae from coastal areas.

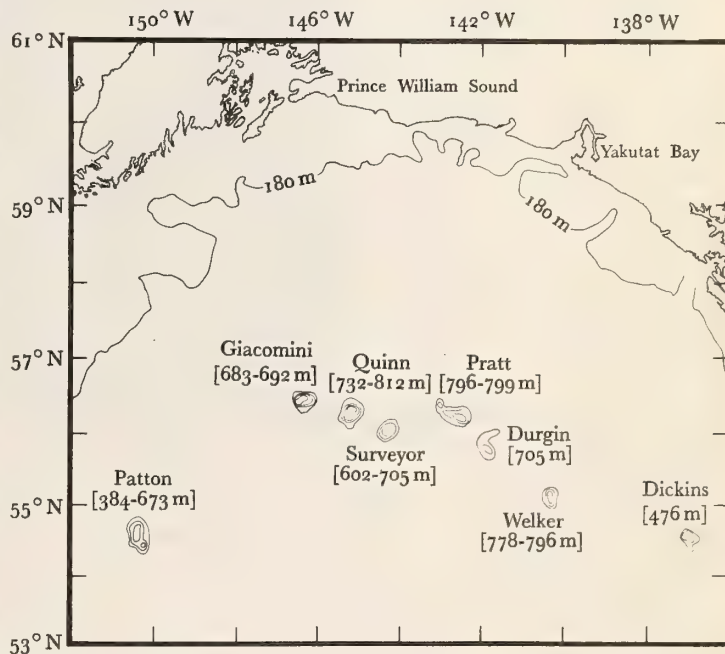


Figure 1

Location of the eight seamounts sampled on the 1979 National Marine Fisheries Service seamount survey. Sampling depths on each seamount are indicated in brackets

The specimens are cataloged (No. 36794) at the Thomas Burke Memorial Washington State Museum, University of Washington, Seattle, Washington.



Figure 2

One of the six Patton seamount specimens of *Fusitriton oregonensis*

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Corbicula fluminea (Müller) on the Delmarva Peninsula

BY

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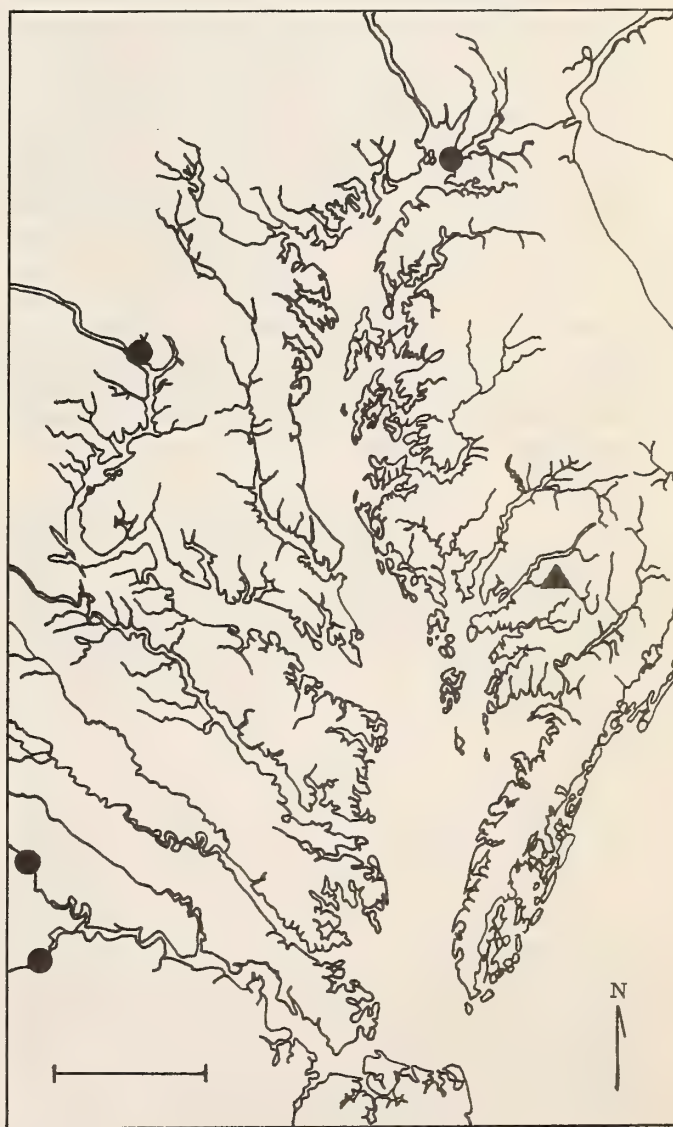
Lewes, Delaware 19958

(1 Text figure)

Corbicula fluminea (Müller, 1774) has been reported from several tidal, freshwater localities in the estuaries of the western shore of Chesapeake Bay (Figure 1). These include the populations reported by DIAZ (1974) in the Appomattox River at its confluence with the James River near Hopewell, Virginia (80 nautical miles from Chesapeake Bay) and populations at Hog Island, Virginia, 30 nautical miles from the bay and the location of the salt front in the James River. DRESLER & CORY (1980) reported *C. fluminea* was collected in 1975 from the tidal Potomac River at Washington, D. C. and they found populations as far down stream as Piscataway Creek, Maryland. Their observations indicated the clam could be found downstream to the location of the salt front at Indian Head, Maryland. STORRS *et al.* (1977) reported specimens taken from Susquehanna Flats from silt-sand to hard sand substrata where no detectable salinity was found. Other specimens from this locality were brought to our laboratory and indicate the population at Susquehanna Flats, near Turkey Point and Havre de Grace, Maryland, have survived in the Chesapeake Bay since 1975 to the present.

Specimens of *Corbicula fluminea* were collected in the Wicomico River at Salisbury, Maryland in June 1979. A sample of these specimens was sent to our laboratory for identification. This represents the first record of the species on the eastern shore of the Chesapeake Bay.

The continued presence of *Corbicula fluminea* at the head of Chesapeake Bay indicates seasonal fluctuations of



(adjacent column →)

Figure 1

Populations of *Corbicula fluminea* in and surrounding Chesapeake Bay. Dots represent reports in the literature and the triangle the new record for Delmarva Peninsula Scale bar = 40 km

salinity have not had a significant effect on survival of these clams. *Corbicula* spp. has been reported from haline estuarine environments not only in the United States (COPELAND *et al.*, 1974; DIAZ, 1974; GAINES & GREENBERG, 1977; GAINES, 1978a, b; EVANS *et al.*, 1979) but also in the Orient (SUNG, 1972; KADO & MURATA, 1974). While evidence from California populations demonstrated a salinity tolerance of 14‰, the ultimate salinity tolerance of Chesapeake Bay populations is incompletely understood. DIAZ (1974) reported collections of *C. fluminea* in the James River where salinity reached 5.5‰. Other populations in the estuaries of the Chesapeake Bay are in either low salinity water or freshwater.

The appearance of *Corbicula fluminea* on the Eastern Shore also raises some questions concerning the dispersion of these clams. The hypothesis that migratory waterfowl transported *C. fluminea* in their gastrointestinal tracts was widely supported for many years (SINCLAIR & ISOM, 1963). However, since the work of THOMPSON & SPARKS (1977) it now seems unlikely that these clams can be transported long distances in this fashion. Mackie (personal communication, 1980) has found that Sphaeriacean clams will survive ingestion by waterfowl only if they are regurgitated shortly after being swallowed. Since other populations of *C. fluminea* are not separated by great distances across the bay, it is not too unreasonable to tentatively attribute the establishment of a population in the Wicomico River by an ingestion-short flight-regurgitation mechanism.

ACKNOWLEDGMENTS

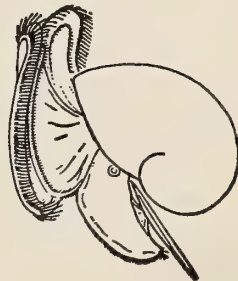
The author wishes to thank Mr. A. Wesche, Maryland Department of Natural Resources and Mr. J. Nelson, National Capital Shell Club for providing specimens and

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University of Delaware College of Marine Studies Contribution No. 158.

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NOTES & NEWS

Another Generous Donation from the San Diego Shell Club

Shortly after our July issue had gone to press, we received a very generous contribution from the San Diego Shell Club. We express our gratitude for this continued support, which is particularly encouraging in these inflationary times with their financial uncertainties.

As in the past, contributions of this sort are added to our Endowment Fund, from which the income materially assists us in our endeavor to keep the subscription rate of the *Veliger*, as well as the membership dues in our Society at the lowest possible level.

IMPORTANT NOTICE

We have been informed by Mr. Art West that he has sold his business. The new owners, Don and Jeanne Pisor, will carry on the business under the name "Seashell Treasures Books." They will, henceforth, handle all orders for back-volumes of "The *Veliger*." The address is: 646 30th Street, San Diego, CA (lifornia) 92102,

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is coming! And although the Postmaster General keeps asserting that its use is entirely voluntary, there are certain consequences to be anticipated if it is not used. One consequence which will affect us directly is the fact that "addressed pieces with the 9 digit code" will be entitled to a discount (this applies to bulk mailings, such as the quarterly dispatch of our journal). In other words, if the code is not used, we have to pay what really amounts to a penalty. Another consequence, which will undoubtedly apply to all mail, will be the fact that "properly coded mail" can be handled more expeditiously. The implication seems to be that those pieces that do not have the new zip code may be subject to delays in delivery.

For these reasons we earnestly ask all our subscribers and members to inform us as early as possible of their correct new zip. Since our mailing list is not on a scale as

as large as those of the various news weeklys, we cannot take advantage of the computer tapes that the Postal Service has prepared and will lend to the volume mailers. We will, of course, endeavor to obtain the correct codes; but we would prefer not to have to spend hours on the telephone obtaining the numbers in that way.

That the Postal Service leaves much to be desired, not only in the United States, but abroad as well, was brought home to us with the delivery of our January issue. Second class mailing requirements make it necessary for us to tie securely the various copies of a particular issue going to a particular country in a bundle with a label of the country of destination. Thus, for example, all copies going to Japan will be tied together (in the case of certain countries we have a sufficiently large number of copies to make several bundles and combine them into a "direct sack"). Yet some individuals in each of the "direct sack"-countries received their copies from several weeks to 2 months later than others. We have, of course and unfortunately, no control over these vagaries of the postal services. Our complaints have no effect whatever.

Publication Date of THE VELIGER

THE PUBLICATION DATE of The *Veliger* is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus, our publication is available in the meaning of the Code of the ICBN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US\$8.00 in all cases where the *Veliger* goes to domestic addresses, and a deposit of US\$25.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

We think it important to bring to the notice of all our actual and potential correspondents that the postal fee for registered articles is the highest in the world: \$3.25, regardless of destination. Further, to certain countries it is not possible to have mail pieces insured or registered. In the cases where the prospective recipient desires our communications sent as registered article, we must expect advance payment of that fee. We are unable to return manuscripts (either for reworking or with the recommendation that they be submitted elsewhere) other than by ordinary surface mail. In view of the ever more deteriorating postal services in most countries, we can obviously not assume any responsibility for the safe delivery of any items we must dispatch. Our responsibility must and does end with our delivery to the post office of any item.

Subscription Rates and Membership Dues

We are pleased to announce that at its annual business meeting the Executive Board of our Society has decided to maintain the subscription rate for volume 24 of *The Veliger* at US\$ 37.50 plus \$1.50 for mailing charges to domestic addresses; however, it is necessary to increase the charge for mailing to all foreign addresses to US\$5.- because the postage rates are scheduled to be doubled in 1981. Also, because many of our subscribers have encountered difficulties in transmitting the necessary funds in Swiss Francs, we have closed our Swiss Postcheck (Giro) account, effective December 31, 1980. Thus, all payments henceforth must be in U. S. funds.

At the same meeting it was also decided to keep the membership dues at the same level as for volume 23, with the mailing charges for domestic addresses at \$1.50 and those for ALL foreign addresses increased to US\$5.-.

Because of some irregularities that have occurred in the recent past, we must stress that membership renewals with the correct amount must reach us on or before April 15 each year; if payment is received after that date, a re-instatement fee of \$1.- is required.

From the foregoing it should be evident that we make a strong effort to combat inflation. But we must ask for cooperation by all our members and subscribers.

Sale of C. M. S. Publications:

Effective September 1, 1981, all back volumes still in print, both paper covered and cloth bound, will be available only from "Seashell Treasures Books," 646 30th Street, San Diego, California 92102. The same applies to the supplements still in print, with certain exceptions (see be-

low). Prices of available items may be obtained by applying to Mr. Pisor at the address given above.

Volumes 1 through 8 and 10 through 12 are out of print.

Supplements not available from Mr. West are as follows:

Supplements to vol. 7 (Glossary) and 15 (Ovulidae) are sold by 'The Shell Cabinet,' P. O. Box 29, Falls Church, VI(rginia) 22046; supplement to vol. 18 (Chitons) is available from 'The Secretary,' Hopkins Marine Station, Pacific Grove, CA(lifornia) 93950.

Supplements

Supplement to Volume 3:

[Part 1: Opisthobranch Mollusks of California
by Prof. Ernst Marcus;

Part 2: The Anaspeidea of California by Prof. R. Beeman, and The Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

Supplement to Volume 6: out of print.

Supplement to Volume 7: available again; see announcement elsewhere in this issue.

Supplement to Volume 11:

[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Volume 14:

[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 16:

[The Panamic-Galapagan Epitoniidae by Mrs. Helen DuShane]

[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]

Supplement to Volume 17: Our stock of this supplement is exhausted. Copies may be obtained by applying to Dr. E. C. Haderlie, U. S. Naval Post-Graduate School, Monterey, CA(lifornia) 93940.

WE ARE PLEASED to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print editions of the publications of the Society. The microfiches are available as negative films (printed matter appearing white on black background), 105 mm × 148 mm and can be supplied immediately. The following is a list of items now ready:

Volume 1 through Volume 6: \$9.00 each.

Volume 7 through Volume 12: \$12.00 each.

Supplement to Volume 6: \$3.00; to Volume 18: \$6.00
California residents please add the appropriate amount for sales tax to the prices indicated.

Please, send your order, with check payable to Opisthobran Newsletter, to Mr. Steven J. Long, 359 Roycroft Avenue, Long Beach, California 90814.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from Mr. Arthur C. West, P. O. Box 730, Oakhurst, CA(lifornia) 93644. Orders should be sent directly to Mr. West.

Single Copies of "The Veliger":

We have on hand some individual copies of earlier issues of our journal and are preparing a list of the various issues available with the prices. Some issues are present in only one or two copies, while others may be present in 10 or more copies. As we are anxious to make room, we will offer these numbers at an exceptionally low price. This list may be obtained by sending a self-addressed, stamped envelope to the Veliger, 1584 Milvia Street, Berkeley, CA(lifornia) 94709. Foreign correspondents should enclose one international postal reply coupon. Requests for the list, for which return postage is not provided, will be ignored.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15 but before March 15 of the following year, there will be a re-instatement fee of \$1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of the remittance. The same policy applies to new members.

THE VELIGER is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject

to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of \$1.- to a percentage of the value of the draft, going as high as 33%. Therefore, we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of First Interstate Bank (formerly United California Bank). This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable, except as indicated elsewhere in this section.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of \$4.25 (to reimburse us for the expenses involved in redeeming them) and at \$0.95 per \$1.- face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Moving?

If your address is changed it will be important to notify us of the new address at least six weeks before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. The following charges must be made:

change of address - \$1.-

change of address and re-mailing of a returned issue

- \$2.75 minimum, but not more than actual cost to us.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

At present we are charged a minimum fee of \$15.00 on each order for new addressograph plates. For this rea-

son we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the Veliger make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time; that is, 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as

insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed \$400.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, \$400.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manuscript, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U. S. A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are submitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript – including figure explanations and the "Literature Cited" section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the "dead letter" office; in other words, it is destroyed.

Policy Regarding Reprints

It seems necessary to bring the following points to the notice of prospective authors:

All manuscripts submitted for inclusion in The Veliger are subject to review by at least two scientists; acceptance is entirely on the basis of merit of the manuscript. Although many scientific journals assess page charges, the

Executive Board of our Society, for the time being at least, wishes to avoid this possible financial handicap to the younger contributors. However, because of the high cost of halftone plates, a suitable contribution to reimburse the Society must be sought.

Similarly, while it was hoped at the "birth" of The Veliger, that a modest number of reprints could be supplied to authors free of charge, this has not as yet become possible. We supply reprints at cost. Unfortunately, in recent years it has become "fashionable" for some authors and some institutions to ignore paying for reprints ordered and supplied in good faith or to delay payment for a year or more. This causes financial losses to the Society since our debts are paid promptly. Since the Society is in fact not making any profit, it is necessary to introduce a policy which, it is hoped, will protect us against negligence or possible dishonesty. In the case of manuscripts from sources outside of the United States, if a manuscript is accepted, we will inform the author of the estimated cost of reprints and require a deposit in U. S. funds to cover these costs. If such a deposit is not made, we will not supply any reprints. In the case of non-payment by domestic authors or institutions, we will pursue legal recourses.

General Notice

Because of an increasing number of strange occurrences your editor deems it important to clarify our policy with respect to correspondence.

1. We never reply to letters that do not reach us. Since the U. S. postal service no longer forwards mail pieces that are not franked properly, correspondents waiting for our reply might consider the possibility that their letter falls into this category.

2. We do not acknowledge the receipt of a manuscript unless a self-addressed, stamped envelope is enclosed.
3. We do not reply to complaints regarding the non-arrival of our journal, if these complaints are made at a time when the claimed issue could not possibly have reached its destination. In view of the poor postal service throughout the world, it is unrealistic to expect, for example, the July issue in a shorter period than from 2 to 3 weeks in the United States, in less than 4 to 6 weeks in Europe, and in less than 2 to 4 months in other areas of the world; South American countries, in particular, have to expect maximum delays. It should be obvious that we are not responsible for the postal service.
4. We particularly object to complaints about non-receipt of issues which are scheduled to be published as much as 6 months after the complaint was sent! A little consideration of what is possible and what is absurd should help to obviate such untimely complaints.
5. We are receiving an increasing number of requests for our list of individual back numbers that are still available, as well as for our suggestions to prospective authors. These requests state that a self-addressed stamped envelope is enclosed — but somehow the writer must have forgotten to do so. These requests also are not answered by us.

We consider that our policy is justified for several reasons: the requirement for self-addressed, stamped envelopes has been stated in every issue of the Veliger for the past several years. Since we are a non-profit organization, we prefer to reserve our energy and our resources for productive purposes. However, we do conscientiously, and usually exhaustively, reply to all correspondence that we consider legitimate. Moreover, such correspondence is usually answered the same day as received, with the reply posted the next morning at the main post office in Berkeley. What happens afterwards is beyond our control.

BOOKS, PERIODICALS, PAMPHLETS

Functional Morphology and Development of Veliger Larvae of the European Oyster, *Ostrea edulis* Linné

by THOMAS R. WALLER. Smithsonian Contributions to Zoology, No. 328; 70 pp.; 152 figs. 10 February 1981

Although there has been a great deal of recent interest in the details of gross morphology of the larval shells of mollusks, particularly on the part of paleontologists who have discovered that larval shells are well preserved in many fossil marine sediments, details of larval development and morphology are virtually unknown for most mollusks. Before we can understand the roles of larval stages in the evolutionary diversification of mollusks, we need to know a great deal beyond simple deductions of major developmental types from larval shell morphology.

Thomas R. Waller's meticulous and beautifully illustrated documentation of the larval morphology of the European oyster is a major contribution to the study of molluscan development. Although the title suggests functional analysis (a more popular form of study these days), the thrust of the paper is, and should proudly be so, descriptive with some interesting and careful functional interpretations woven in.

Waller has anesthetized, fixed, and critical point dried living oyster larvae at a variety of stages of development. His preparations are excellent and his description of morphology and development is richly illustrated with 141 scanning electron micrographs of shells, shell structure, and details of anatomy, including ciliation of the velum, development of the foot, major openings on the foot and body wall, development of gill primordia, and early development of sensory structures.

Descriptive and comparative morphology are not particularly popular these days, although we now have the technological advances to enable us to do elegant studies of form, structure, and development. When functional and evolutionary hypotheses are integrated into such studies, they are potentially among the most valuable and lasting contributions that biologists and paleobiologists can make.

Carole S. Hickman
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Berkeley, CA 94720

Malacological Review

Vol. 13: iv + 204 pp.; many illustr.; 1 color plate. 1980

This volume, just as all its predecessors, includes several original papers, some of a few pages, some brief notes and reproductions of tables of contents of various malacological periodicals. There is, however, a very important article, starting on page 121 and ending on page 143. It is, in essence, a key to the freshwater snails of the Philippines. The importance of this paper by J. B. Burch lies in the fact that there are many parasitic diseases for which mollusks are intermediate hosts. The most efficient way to short-circuit the life cycles of parasites is the control of the intermediate hosts. And in order to know the most appropriate approach to such controls, it is necessary to know the intermediate hosts. The title of this paper is "A guide to the freshwater snails of the Philippines." Into the same category belongs the paper by F. Frandsen, F. McCullough & H. Madsen, "A practical guide to the identification of African freshwater snails," on pp. 95 to 119.

It does not come as a surprise that this publication is forced to increase its subscription rate as announced on p. ii. The surprise, however, is the modest amount of the increase from \$17.- to \$19.- for institutions and from \$10.- to \$11.- for individuals. Also announced is a change of address for the publication to P. O. Box 2750, Ann Arbor, Michigan 48106, U. S. A.

R. Stohler

Cone Shells from Cape Verde Islands**A Difficult Puzzle**

A look at the workshop of evolution.

by D. RÖCKEL, E. ROLÁN & A. MONTEIRO; privately published. Available in the U. S. A. from Seashell Treasures, Don & Jeanne Pisor, 646 30th Street, San Diego, California 92102, U. S. A. Price on request from Mr. Pisor. 156 pp., 8 color plates; 131 text figures. ISBN 300-3993-7.

January 1980

This book is the result of the collaboration of several dedicated serious amateurs. From the work it appears that the Cape Verde Islands are especially rich in endemic species and varieties of cones. The relative restraint of the authors in naming only 5 new species and 2 new subspe-

cies is admirable. Of one species, *Conus cuneolus* Reeve, 1844, they distinguish 13 forms, labeled simply alphabetically. The only serious flaw in the work is the fact that no type locality is expressly and formally listed; this may be a minor drawback in most cases as small maps indicate the localities where the specimens were collected; however, in some cases specimens in the type lot were collected in different spots and no indication is made as to the exact provenance of the holotype.

In spite of this slight flaw, the book is an excellent example of what a group of dedicated amateurs with a good supply of "stick-to-it-iveness" can accomplish. The vast fraternity of cone collectors should welcome this book as a stimulating adjunct to their libraries.

R. Stohler

Beiträge zur Kenntnis der Olividae

Acta Conchyliorum No. 1; Club Conchylia publisher. English Edition. 201 pp.; 28 plates of color photographs. DIETMAR GREIFENEDER, with contributions by R. Wittig-Skinner, M. Widmer & J. Hemmen.

English version available from Seashell Treasures, Don & Jeanne Pisor, 646 30th Street, San Diego, California 92102.

This book is a very interesting approach to a study of a group of species that produce extremely variable shells. Olividae are very attractive because of their rich colors and highly polished shells. In this book, after a generalized introduction, the three contributors discuss and describe habitats of three distinct geographical areas: Indonesia, Dar es Salaam and Jaco/Costa Rica. We get a clear picture of the populations that were studied and the documentation is superb — color photographs in original photographic prints — not reproduced through color pictures which would involve the complex and costly printing process with its inherent difficulties of correct color rendition. This is not to imply that the color prints are less costly, but in the relatively small edition which this work has experienced, it is the less costly approach. Of course, the expense of producing this book is relatively great but the price of the book is relatively modest (we believe it

will be about \$40.-) and should not keep any true Olividae lover from acquiring it. For it truly is the next best thing to having the shells themselves.

R. Stohler

Hawaiian Nudibranchs

by HANS BERTSCH & SCOTT JOHNSON. ISBN 0-932596-15-0. 112 pp.; 134 color illustrations. Oriental Publishing Co., P. O. Box 22162, Honolulu, Hawaii 96822. \$6.95 plus \$0.59 handling charges. April 1981

This scientifically accurate account is written with the interested layman in mind. But nevertheless, an error of judgment, made in most similar publications, is here carefully avoided: no "common names" have been invented for these stunningly beautiful animals. For this judicious restraint we commend the authors.

The price of the book is surprisingly low considering the high quality of the color reproductions and today's printing cost. It is doubtful that the authors will become millionaires on the royalties from the sale of this work.

R. Stohler

Freshwater Mollusks of California: A Distributional Checklist

by DWIGHT W. TAYLOR. Calif. Fish & Game 67 (3): 140-163 July 1981

This systematically arranged list of 91 species of bivalves and gastropods includes accounts of a few species that inhabit brackish water and coastal intertidal forms. For each species a complete and correct citation is followed by a listing of the type locality (if known), range and distribution, and habitat; in some cases, 'Status,' 'Threats' and synonyms are given.

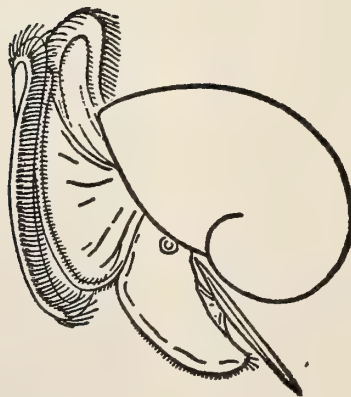
R. Stohler

**Tropical Eastern Pacific Limpets of the Family
Acmaeidae (Mollusca, Archaeogastropoda):
Generic Criteria and Descriptions of Six New Species
from the Mainland and the Galápagos Islands**

by DAVID R. LINDBERG & JAMES H. McLEAN. Proc. Calif.
Acad. Sci. 42 (12): 323-338; 34 figs. (24 June 1981)

Four new species of *Notoacmea* and two of *Lottia* are described. Of these, 2 *Notoacmea* and both *Lottia* species are endemic to the Galápagos Islands.

R. Stohler



THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in **THE VELIGER** is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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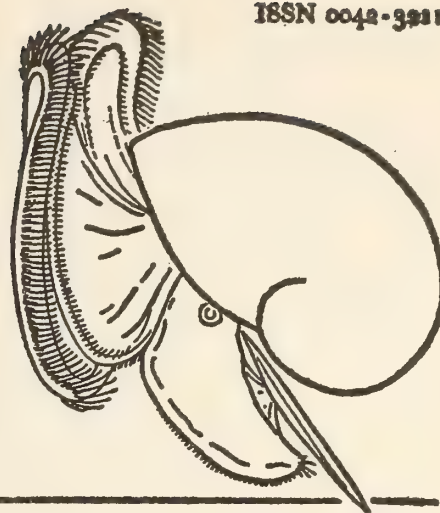
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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
 SUPERFAMILY, FAMILY, Subfamily, Genus, (Subgenus)
New Taxa

Taringa aivica timia Marcus & Marcus, 1967

(Nudibranchia : Doridacea)

in California

BY

DAVID W. BEHRENS

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AND

ROBERT HENDERSON

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(4 Text figures)

BEHRENS (1980: 102) reports a *Taringa* sp. (indet.) from Palos Verdes, California. It was originally thought to be an undescribed species. However, close examination of the specimen and comparison with the 6 worldwide species suggest that the animal is *Taringa aivica timia* Marcus & Marcus, 1967. To date it is reported from Puerto Peñasco, Sonora, Mexico (MARCUS & MARCUS, 1967; KEEN, 1971).

On April 30, 1979, Mr. Robert Henderson collected a single specimen in 10 m of water 0.8 km east of Paradise Cove, Los Angeles County, California (Lat. 34°0'2"N; Long. 118°47'2"W). The living animal measured 33 mm long, 28 mm preserved, and matched the original description closely. A brief description of this specimen is presented here to supplement the original description.

DESCRIPTION OF SPECIMEN

Its body was typically doridiform, oval, with a rounded tail which did not extend beyond the notum (Figure 1). The notum was convex, highest along the midline, sloping gradually to the margins. The entire dorsal surface of the notum was covered with villous papillae, interspersed with larger inflated papillae of various sizes. In life, the large papillae were irregular and variable in shape and size (Figure 2). There were 16-18 papillae which were equally distributed laterally on the notum. The notal spicules were present subcutaneously and did not protrude from the notum or papillae. The spicules were smooth,

straight or slightly curved rods (Figure 2). Within the notum they were relatively sparse, and deep cutaneously. They appeared to form no matrix within the notal tissue. Papillae contained very few, if any, spicules. When present, they did not break the notal surface.

The anterior margin of the foot was truncate and bilabiate. The foot measured 9 x 24 mm, and the margins were parallel. The labial tentacles were long in life; when preserved, they were 2.5 times as long as wide and tapered to pointed tips. The tentacles arose independently on either side of the mouth, but were closely adjacent to it.

The body color was dusky yellow. Patches of white and dark brown were dispersed over the notum. Darker areas appeared through zones of fewer papillae. A few irregularly shaped white blotches were present on the notum; however, white flecks were more prevalent on the papillae. There were also brown flecks, which were restricted to the surface of the notum and absent from the papillae. Larger white specks were prominent on the 4 to 6 largest papillae. A subtle cream colored line connected the rhinophoral pits. The same color was found in concentrations of flecks at 3 or 4 equally spaced points along the notal margin. Two rust colored spots were observed on the notum. The sole of the foot was yellow with several small dark-brown spots. The hyponotum and sides of the foot were cream with a few brown spots and flecks. The rhinophores were also cream colored, with large white spots on the posterior of the stalk near its base. The clavus was vertically striped and spotted with brown. The tip of the

clavus was white. The branchiae were cream with brown flecks.

The rhinophores were long, measuring 3.5 mm. They retract into fluted upright sheaths. The stalk was about one-third the length of the rhinophore. The clavus was deeply perfoliate with 17 diagonal lamellae. An anterior cleft existed up through the penultimate lamella; the ultimate lamella was entire. The distance between the rhinophores was equal to their distance from the margin, both laterally and anteriorly.

The branchial plume was completely retractile into a fluted branchial pit. The 6 tripinnate branchiae were up-

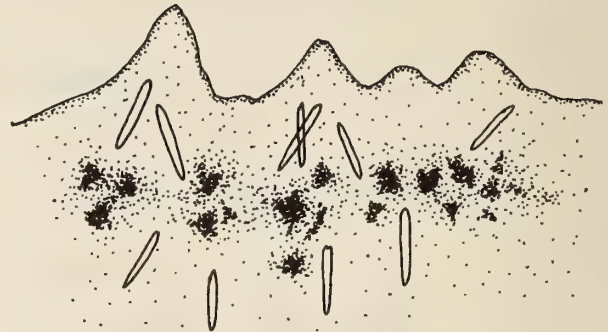
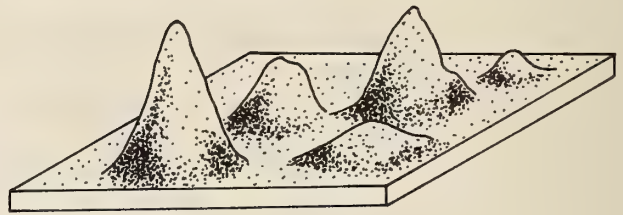
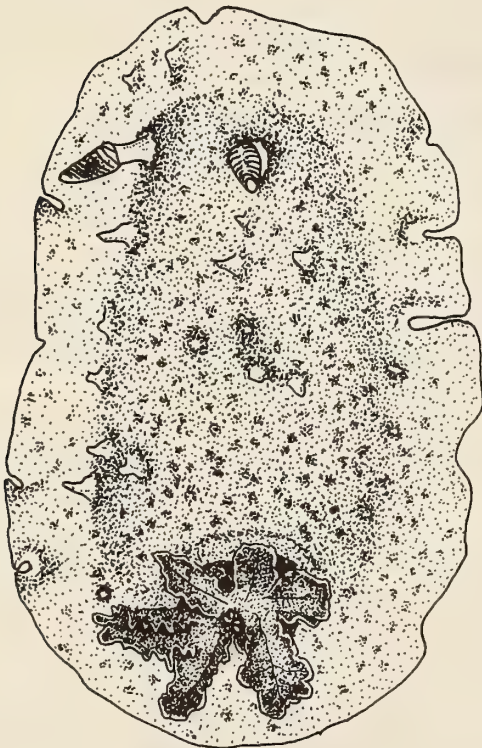


Figure 2

Plain view and cross-section of the notal surface of *Taringa aivica timia* showing papillae and spicules



standing and did not spread to the edge of the notum. They were situated around an anal papilla which was distally fluted into 8 lobes.

The radular formula was $31 \times 4-5.36-39.0.36-39.4-5$ at about the 15th row. The laterals were hamate with a high base. They increased in size to the mid-point of the row, and then decreased to the margin (Figure 3a). All, except the innermost few, had a row of 5 to 10 pointed denticles on the outer side of their cusp (Figure 3b). The marginals were pectinate (Figure 3c). No labial armature was noted. MARCUS & MARCUS (1967) report the radular formula to range from $29-41 \times 4-6.44-70.0.44-70.4-6$.

The genital opening was located on the right side of the body. The penis was armed with a chitinous bell-shaped cuticle (Figure 4). This character is perhaps the most diag-



(← adjacent column)

Figure 1

Dorsal and lateral views of *Taringa aivica timia*

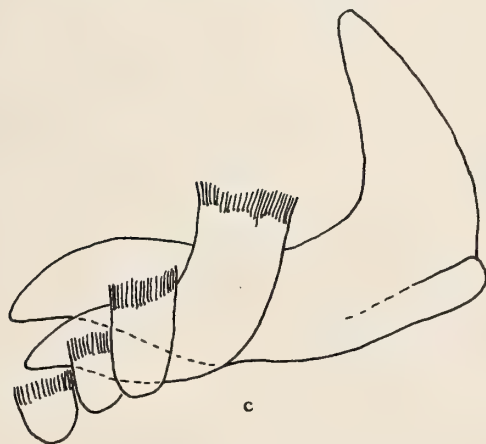
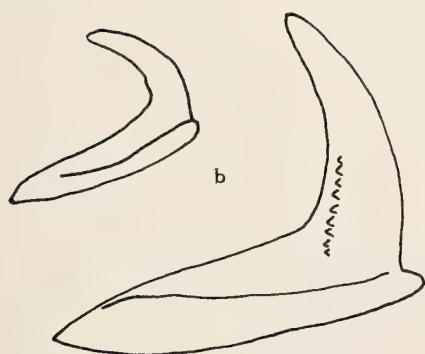
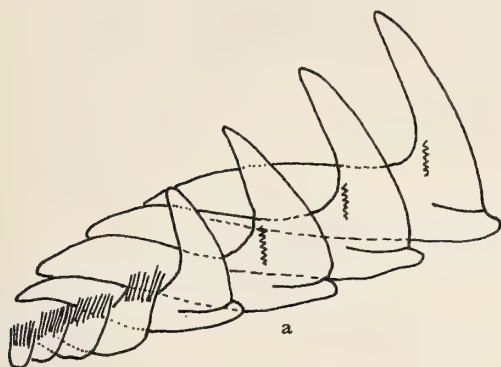


Figure 3

Radula of *Taringa aivica timia*

- a. portion of lateral series
- b. hamate laterals
- c. pectinate marginals

nostic of the genus (MARCUS, 1955; MARCUS & MARCUS, 1967).

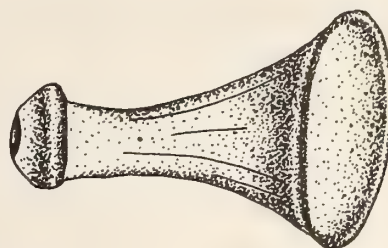


Figure 4

Genital armature of *Taringa aivica timia*

The specimen was found in a kelp holdfast on the sponge *Zygherpe hyaloderma* deLaubenfels, 1932.

On this coast *Taringa aivica timia* might be confused with *Discodoris heathi* MacFarland, 1905, were it not for the irregularly large inflated notal papillae which do not occur in *D. heathi*, the radular morphology and the penis armature.

Color transparencies of the living animal are on file at California Academy of Sciences (CASIZ No. 3726), Los Angeles County Museum, and Santa Barbara Museum of Natural History (SBMNH No. 00004SL).

ACKNOWLEDGMENTS

Many thanks to Karen Green for identification of the sponge, to Lorraine Bemis for her assistance in sorting through kelp holdfasts in search of this species, to Mari-beth DeMeo for help in preparing the manuscript and especially to Dr. Rim Fay for his immeasurable input.

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The Gastropoda and Sphaeriacean Clams of Red River, Kentucky

BY

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(1 Text figure)

INTRODUCTION

THE RED RIVER of northeastern Kentucky, a major tributary of the Kentucky River, is an exceptional stream geologically, aesthetically, biologically, and politically. Following an intensive environmental campaign to save the stream from a planned U.S. Army Corps of Engineers dam, the north fork of the stream was set aside as a part of the Wild and Scenic Rivers system. The middle fork of the stream runs through Natural Bridge State Park, and the smaller south fork drains timber and farmlands. Although the river has retained a large percentage of the Upper Kentucky River fish fauna (BRANSON & BATCH, 1974), the stream does not offer particularly good habitat conditions for gastropods, mostly because of little aquatic vegetation and low dissolved bicarbonates. Molluscan investigations in the drainage are few. HOUP (1980) recently surveyed the unionid mussels of the North Fork of Red River. BRANSON & BATCH (1969) reported *Corbicula* from the mouth of the main Red River and conducted an extensive study of terrestrial and aquatic gastropods of one Red River creek system, including three stations on the Middle Fork of the Red River (BRANSON & BATCH, 1970). The present contribution reports the gastropods and sphaeriacean clams collected during a fish survey of Red River (BRANSON & BATCH, 1974). Considering the size of the stream, the fingernail clam and gastropod fauna must be judged depauperate; only two families, two genera and three species of sphaeriacean clams and three families, five genera and seven species of gastropods were collected. The bulk of the collections was secured from lower segments of the river, *i.e.*, streams running through third order valleys or larger. A total of 33 stations were visited

(Figure 1) but specimens were discovered at only 15 of them.

COLLECTING STATIONS

Red River heads in Clark and Estill counties, Kentucky and mainly flows through Wolfe, Powell and Minifree counties, nearly all in Daniel Boone National Forest. The drainage encompasses approximately 460 square miles (1190 km²); the largest stretch of stream is about 75 km. Aquatic vegetation is sparse to lacking in first through third order streams, whereas the lower sections of the river (order 4 through 6) support stands of *Nitella*, *Nasturtium* and *Dianthera*. These conditions are reflected in the collections, many of the upper stations being very depauperate in specimens.

The 33 collecting stations visited were each approximately 0.3 km long and were selected to include as many habitat types as possible. All stations are included below whether snails were found or not, since negative data are often as important as positive.

Station 1. North Fork of Red River, order 3; 9-15 m wide and 0.6-1.2 m deep; bottom of sand and slate rocks; no vegetation. 8 October 1966.

Station 2. North Fork of Red River, order 4; 4.5-6.2 m wide with 3 cm deep riffles and 1.4 m deep pools; bottom of organic debris and limbs. 8 October 1966.

Station 3. North Fork of Red River, order 4; conditions as those at Station 2. 8 October 1966.

Station 4. North Fork of Red River, order 4; 21-24 m wide with 5-46 cm deep riffles and 0.6-1.2 m deep pools; *Dianthera* on riffles; bottom of sandstone slabs, boulders, bedstone, and sand. 21 October 1966.

¹ Supported by Eastern Kentucky University Faculty Grant

² Dean, College of Natural and Mathematical Sciences

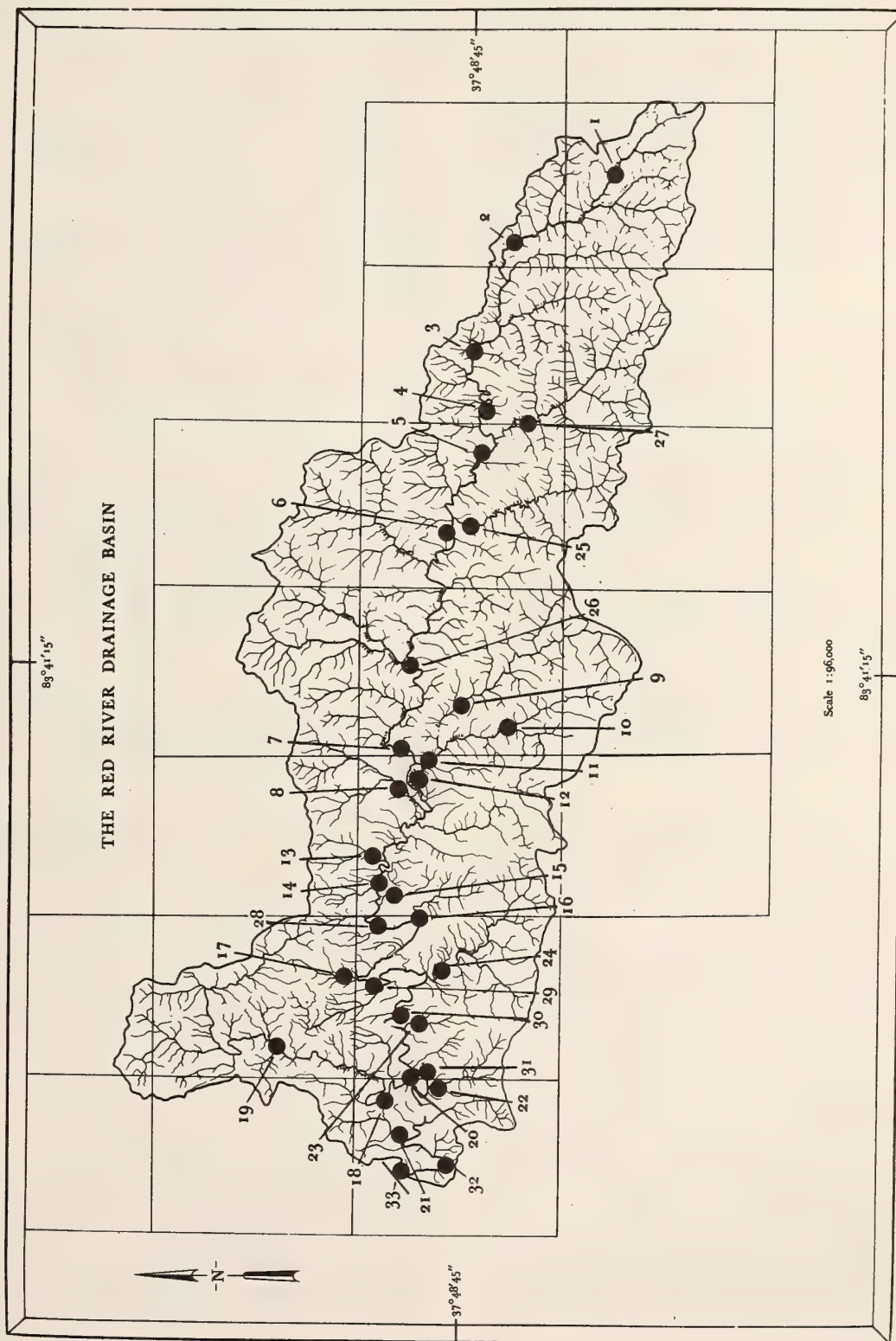


Figure 1

- Station 5. North Fork of Red River, order 4; 12-30 m wide with 10-46 cm deep riffles and 1.8 m deep pools; *Dianthera* on riffles. 21 October 1966.
- Station 6. North Fork of Red River, order 4; 12-30 m wide with 3.6-46 cm deep riffles and 0.6-2.5 m deep pools; bottom of sandstone rocks and sand; *Dianthera* on riffles. 21 October 1966.
- Station 7. North Fork of Red River, order 4; 30-43 m wide with 2-60 cm deep riffles and 0.9-1.5 m deep pools; bottom of small pebbles, gravel and sand. 29 October 1966.
- Station 8. Cane Creek, order 3; 3-6 m wide with 25-50 cm deep riffles and 1.1 m deep pools; bottom of small stones, gravel, debris, clay, silt; no aquatic vegetation. 29 October 1966.
- Station 9. Middle Fork of Red River, order 4; 6-9 m wide with 0.3-1.2 m deep riffles and 0.6-1.2 m deep pools; bottom of small stones and sand; *Dianthera* and *Cladophora* on riffles and *Potamogeton* in pools. 26 November 1966.
- Station 10. South Fork of Red River, order 3; 3-6 m wide with 7.5-20 cm deep riffles and 0.6-1.5 m deep pools; bottom of gravel, rocks and sand; *Cladophora* abundant. 26 November 1966.
- Station 11. South Fork of Red River, order 4; 6-7.5 m wide with 20-28 cm deep riffles and 0.6-1.8 m deep pools; bottom of small rocks, gravel and sand; *Cladophora* abundant. 26 November 1966.
- Station 12. Red River below junction of North and Middle Forks, order 4; 15-18 m wide with 30-106 cm deep riffles and 2.4-3.0 m deep pools; bottom of gravel, rocks and sand; *Dianthera* along margins; current very swift. 17 December 1966.
- Station 13. Hatcher Creek, order 2; 7.6-10.5 m wide with 20-25 cm deep riffles and 0.6-0.9 m deep pools; bottom of gravel, small stones, clay, mud and debris. 17 December 1966.
- Station 14. River at flood stage; impossible to collect. 29 October 1966.
- Station 15. Judy Creek, order 3; 0.9-2.5 m wide with 5-25 cm deep riffles and 0.6-1.8 m deep pools; bottom of mud, gravel, rocks, sewage refuse; bluegreen algae and *Dianthera*. 4 March 1967.
- Station 16. Hatton Creek at mouth, order 5; 1.5-6 m wide with 12.7-30 cm deep riffles and 0.6-2 m deep pools; bottom of silt, mud, sand, leaves and woody debris. 4 March 1967.
- Station 17. Black Creek, order 4; 3-12 m wide with 7.5-46 cm deep riffles and 0.6-1.2 m deep pools; bottom of gravel and rocks, silt and mud in pools. 3 November 1967.
- Station 18. Lulbegrud Creek, order 4; 10.5-12 m wide with 0.6 m deep riffles and 1.5 m deep pools. 3 November 1967.
- Station 19. Lulbegrud Creek, order 3; 9-18 m wide with 7.6 cm deep riffles and 0.6-2.5 m deep pools; bottom of gravel, shale, rocks and sand; *Dianthera* on riffles. 24 March and 23 November 1967.
- Station 20. Lulbegrud Creek at mouth, order 4; 6-7.6 m wide with 15-76 cm deep riffles and 1.2-1.8 m deep pools; bottom of mud, gravel and rocks. 1 April 1967.
- Station 21. Log Lick Creek, order 3; 3-4.6 m wide with 7.6-15 cm deep riffles and 0.3-0.5 m deep pools; bottom of rocks, mud, gravel, sand and debris. 1 April 1967.
- Station 22. Twin Creek, order 4; 3-6 m wide with 7-15 cm deep riffles and 0.9-1.8 m deep pools; bottom of bedrock, rocks, mud and debris. 29 April 1967.
- Station 23. Plum Creek at mouth, order 2; 3-7.6 m wide with 7.6-15 cm deep riffles and 0.2-6.0 m deep pools; bottom of sand, silt, mud, gravel and bedrock. 29 April 1967.
- Station 24. Hardwick Creek, order 3; 6-12 m wide with 25-76 cm deep riffles and 0.6-2 m deep pools; bottom of sand, gravel and debris. 13 May 1967.
- Station 25. Swift Camp Creek, order 3; 6-9 m wide with 25-76 cm deep riffles and 0.6-2 m deep pools; bottom of gravel, rocks, sandstone and sand. 13 May 1967.
- Station 26. Indian Creek, order 4; 4.6-7.6 m wide with 46 cm deep riffles and 0.6-1.8 m deep pools; bottom of rocks, bedrock, sand and silt. 27 May 1967.
- Station 27. Stillwater Creek, order 3; 7.6-10.6 m wide with 30-61 cm deep riffles and 0.8-1.6 m deep pools; bottom of silt, sand, rocks and bedrock. 27 May 1967.
- Station 28. Red River, order 5; 37-43 m wide with 15-25 cm deep riffles and 0.6-2.4 m deep pools; bottom of gravel, sand and rocks; *Dianthera* and algae on riffles. 10 June 1967.
- Station 29. Red River, order 5; 49-55 m wide with 25-90 cm deep riffles and 0.6-2.5 m deep pools; bottom of gravel, flat rocks, logs and limbs, debris and sand; extensive beds of *Dianthera*. 6 October 1967.
- Station 30. Red River order 5; 30-37 m wide with 20-76 cm deep riffles and 0.8-1.8 m deep pools; backwaters

with *Spirogyra*, riffles with *Dianthera* and *Cladophora*. 18 June 1967.

Station 31. Red River, order 5; 20-24 m wide with 15-25 cm deep riffles and 0.6-2.4 m deep pools; bottom of gravel, rocks, mud, debris and logs. 1 July 1967.

Station 32. Red River, order 6; 23-26 m wide and 1.8-4.6 m deep; bottom of mud, gravel, sand and organic debris. 15 July and 12 August 1967.

Station 33. Red River at mouth (on Kentucky River), order 6; 20-24 m wide, 4.9 m deep; bottom of mud, gravel, debris and logs; no vegetation. 12 October and 23 November 1967.

ANNOTATED LIST

Corbicula fluminea (Müller)

Collections: Station 33.

To arrive at this point, this aggressive Asian clam had to migrate through a series of navigation locks on the Kentucky River. Since the collections reported here, the senior author has also observed *Corbicula* below the union of the North and Middle Forks of Red River.

Sphaerium fabale Prime, 1851

Collections: stations 12(8); 18(8).

At both sites, this clam was removed from gravel and sand in beds of *Dianthera*. The current was moderate to swift, the water well-oxygenated.

Sphaerium striatinum (Lamarck, 1818)

Collections: stations 3(2); 18(29); 25(3); 30(1); 31(1).

The most widespread and abundant fingernail clam in Kentucky, this species occupies riffles with moderate to swift current.

Campeloma crassula Rafinesque, 1819

Collections: stations 30(1); 32(6); 33(3).

Seldom encountered in headwater situations, this species was invariably found burrowing in soft mud, often about the roots of *Dianthera*.

Goniobasis semicarinata (Say, 1829)

Collections: stations 7(2); 8(1); 18(76); 19(13); 20(6); 23(1); 25(148); 28(7); 29(30); 30(5); 32(17).

The most abundant and widespread pleurocerid in the Kentucky River basin, *G. semicarinata* also occurs in the Cumberland River basin, particularly in the Little South Fork of the Cumberland. The species typically avoids

headwater streams, being most abundant in riffles with solid substrate.

Pleurocera acuta Rafinesque, 1831

Collections: 23(1); 31(3).

This large, handsome species has become progressively scarce in Kentucky. It is being considered for a Special Concern designation by the Kentucky Nature Preserves Commission (Melvin Warren, Pers. Comm.). There are a few healthy populations below lock nine in the Kentucky River.

Pleurocera canaliculatum (Say, 1821)

Collections: 29(1); 30(2); 32(2).

Lithasia obovata (Say, 1829)

Collections: 31(2).

Lithasia obovata is poorly understood in Kentucky. It has not previously been reported from the Upper Kentucky River basin, where it is apparently rare.

Helisoma anceps (Menke, 1830)

Collections: 29(4); 30(7).

As ubiquitously distributed as *H. trivolvis* is, we were surprised by its apparent scarcity in the Upper Kentucky River basin tributaries. We did not find it in Tight Hollow Creek (Branson and Batch, 1970).

Physa integra Haldeman, 1843

Collections: Station 15(3).

Physa integra is apparently the only representative of the family in the Red River drainage.

DISCUSSION

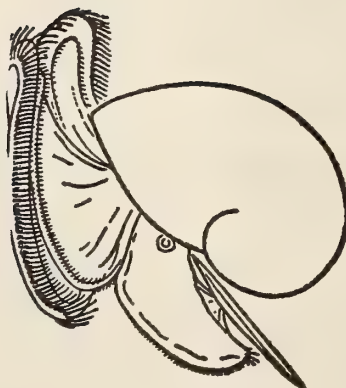
The Upper Kentucky River basin is very poorly productive of aquatic sphaeriids and gastropods, an observation confirming SHOUR's (1943) findings in streams flowing over Lee Formation sandstone in Tennessee. These waters are very low in bicarbonates (11 to 25 ppm) until third order or larger streams are encountered, where the bicarbonate concentration increases to 40 ppm or above (BRANSON & BATCH, 1970). Furthermore, the upland streams have a scarcity of rooted aquatic vegetation, a factor which also militates against an abundant gastropod fauna.

ACKNOWLEDGMENT

We are grateful to Professor William Adams of the Department of Geography, Eastern Kentucky University, for preparing the map.

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linity of streams. *The Nautilus* 56 (4): 130-134



Computer Graphic Analysis of Stereo Micrographs as a Taxonomic Tool

BY

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(1 Plate)

INTRODUCTION

SHAPE IS FREQUENTLY IMPORTANT in taxonomic discrimination. In molluscan taxonomy shape traditionally has been described in qualitative terms; however, classical shape description vocabularies are rife with ambiguity.

In order to make quantitative and statistical analyses of both inter- and intra-species variation, it is necessary to develop a vocabulary of quantitative shape descriptors. Quantification of morphology in molluscan systematics has involved primarily morphometric analyses, in which comparisons are made of linear distances between homologous points or landmarks (see GOULD, WOODRUFF & MARTIN, 1974; KOHN & RIGGS, 1975; GALLER & GOULD, 1979). There is a large body of literature dealing with shape description, both for morphology with obvious landmarks and for forms lacking reliable homologous landmarks. It is possible, particularly with the aid of a computer, to describe shape without reference to landmarks. This is particularly important for describing curvatures and can be done easily from digitized photographic images.

In fact, the capabilities for storing and analyzing complex three-dimensional morphology need not even involve intermediate photographic images. Hardware and software have developed to the point where computers can be programmed to examine objects directly. The use of these more sophisticated forms of technology awaits collaboration between taxonomists and computer software specialists in major academic and industrial settings.

However, the proliferation of low-cost, easy-to-use, microcomputers has placed an important taxonomic tool in schools and homes throughout the country. Three-dimensional data from paired stereo micrographs can be analyzed and stored in a variety of ways (MINTER & PILLER, 1979; ROBERTS & PAGE, 1980). And special-purpose graphic

analysis programming provides a ready-made set of tools for the taxonomist who lacks programming skills.

As a test and simple illustration of the potential of computer graphic analysis in molluscan research, we selected a stereo pair of the radula of an unusual patellacean limpet. The animal is an undescribed species (Lindberg & Hickman, in prep.) of the genus *Pectinodonta* Dall, 1882, a group of deep-sea limpets that live on water-logged wood and ingest wood using a highly modified form of docoglossan radula. The curvature of the teeth is of potential importance not only in taxonomic characterization of the new species but also in understanding the mechanical function of the tooth as an inferred wood rasp.

A direct lateral view of the curvature of an individual tooth is not possible from the flat-mounted specimen illustrated in Figures 1 and 2. We used the information contained in the vertical stereo pair to plot the curvature on the computer video display and then asked the computer to determine the equation for the curve. This provides a description of shape as a set of coefficients of a best-fit power series curve that can be stored numerically. A scanning electron micrograph of a separate preparation (Figure 4) provides a check on the computer results.

METHODS

The computer used is an Apple II equipped with two disc drives, video display, and a graphics tablet (Apple Computer, Inc., Cupertino, CA). The Apple Topographic Analysis Program (Scientific Microprograms, Raleigh, N. C.) was modified for our application by Lane Associates (5324 Selma, Fremont, CA).

Figures 1 and 2 were placed on the graphics tablet, and information on the scale and angular separation of the

stereo pair (7°) were entered into the computer. Using the graphics tablet stylus, the X-Y coordinates of corresponding points on the top of a selected tooth were then entered. The lateral displacement (parallax) of a point in a stereo pair is determined by its Z-axis height (ROBERTS & PAGE, 1980; HOWELL & BOYDE, 1980). After all points were entered, the computer was asked to: 1) plot their Z-axis location, 2) fit a curve to the points as they lay along the crest of the tooth, and 3) display the coefficients of that curve.

RESULTS

Figure 3 shows the plot of the tooth curvature as it appears on the computer video display for comparison with the curvature of the dissected individual tooth in Figure 4. The small size of the paired micrographs (8×11 cm) and the limited resolution of the Apple graphics tablet produces a point spread that could be reduced by using larger prints and a better digitizer. However, the computer-generated curve shows an obvious correspondence to the curve of the dissected tooth. The computed coefficients, $A(0) = 5.492$, $A(1) = 0.660$, and $A(2) = -0.001$, allow straightforward storage of the curve in the computer along with other taxonomic data. The equation into which these are fitted to produce the curve is:

$$y = \sum_{n=0}^{\infty} A_n x^n.$$

IMPLICATIONS

The illustration provided here has several important implications for molluscan taxonomists. First, shape description has, in the past, and particularly for curves and complex shapes, been verbal and highly subjective (see HICKMAN, 1976: 22-23). It can be described in simple mathematical terms and stored for subsequent analyses, such as comparisons of homologous shapes in other individuals or taxa. For the wood-ingesting limpet, *Pectinodonta*, which has a radula that differs markedly from the typical

docoglossate radula of other patellacean limpets, curvature of the unusual, serrate, diagonally arrayed teeth is expected to be helpful in subsequent analysis of tooth function relative to feeding substrates. It will also be very useful to know whether the curvature varies among species of *Pectinodonta*, or (as one might predict if curvature is tightly correlated with function as a wood rasp) if it is constant within the genus.

Second, precise descriptions of shape can be derived from stereo photographs or stereo scanning electron micrographs of complex three-dimensional objects. Scanning electron micrographs provide the standard method of storing a great deal of two-dimensional data about very small objects. But inferences of depth and contour in scanning electron micrographs are subjective, and a single micrograph is not a good source of quantitative information. Stereo micrographs are essential to an understanding of radular morphology (HICKMAN, 1977; 1980), but interpretations remain subjective: quantification from stereo pairs is not an easy matter without the aid of computer graphics.

Perhaps the greatest potential of the computer graphics revolution with respect to taxonomic analysis from stereo pairs is the freedom that it allows to view small complex objects from alternative vantage points. In this study, we simply recorded points on a selected line and obtained a curvature, enabling us to see a tooth from the side rather than looking directly down on it. If additional points are plotted, entire objects can be mapped and viewed from a variety of other angles. Dimensions, areas, and volumes can be obtained, stored, and compared.

The software used in this analysis is also capable of the same kind of analysis using serial sections in place of stereo photographs, providing an application in the study of the anatomy of soft parts.

Taxonomists traditionally have spent a great deal of time in both the measurement of specimens and in the analysis of measurements. Computer graphic techniques not only offer important shortcuts in the analysis of quantitative data, but they can also facilitate the time-consuming process of making measurements in the first place.

Explanation of Figures 1 to 4

Figures 1 and 2: Stereo micrographs of the flat-mounted radula of an undescribed species of the wood-eating limpet *Pectinodonta*. Angular separation of micrographs = 7° . Bar = 100 μ m.
Figure 3: Plot of curvature of individual tooth from computer

video display for comparison with actual curvature of tooth in Fig. 4.

Figure 4: Side view of a preparation of a single tooth, illustrated at the same magnification as the video display plot in Fig. 3.

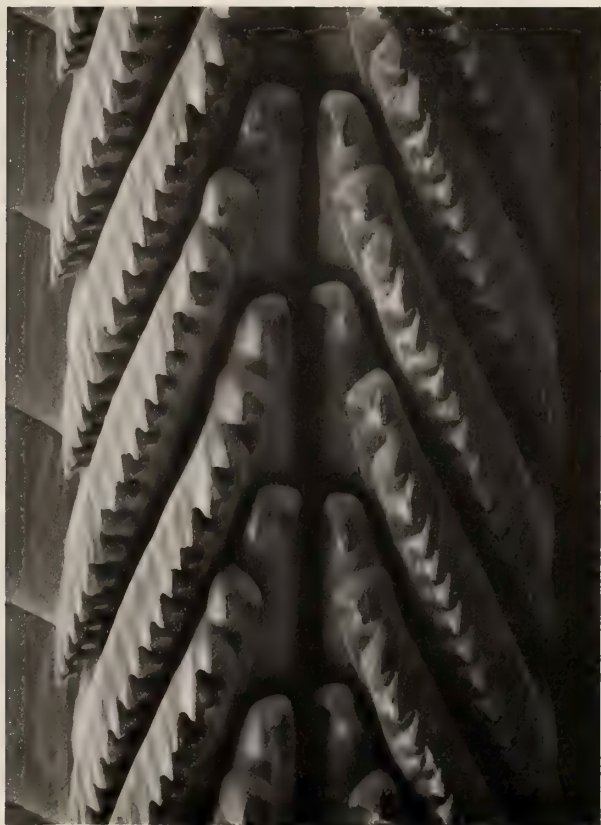


Figure 1

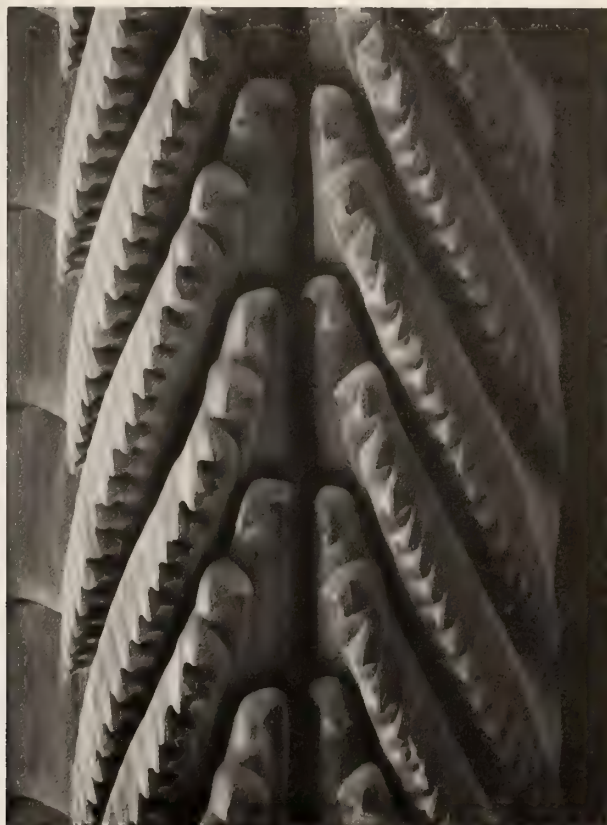


Figure 2

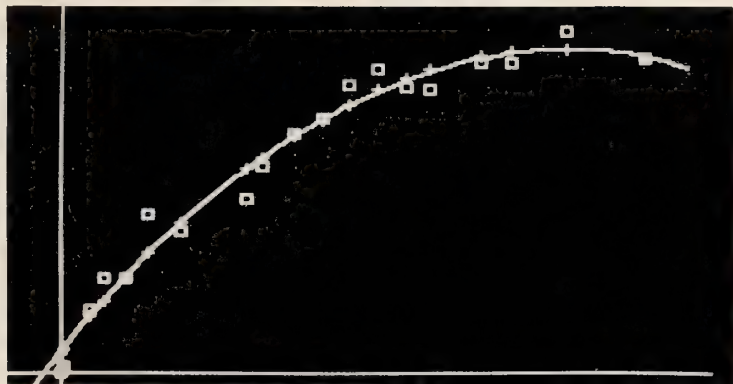


Figure 3



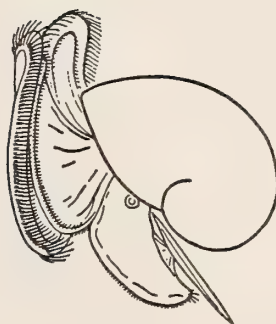
Figure 4

ACKNOWLEDGMENTS

This research was supported in part by National Science Foundation Grants DEB 77-14519 and DEB 80-20992 to CSH. Scanning electron micrographs were taken at the U. C. SEM Lab (Cambridge 150 Stereoscan). The specimens for radula preparation were provided by Eve Southward, Marine Biological Association of the United Kingdom.

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Three New Species of Dorid Nudibranchs

(Gastropoda : Opisthobranchia)

from the Hawaiian Islands

BY

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(2 Plates; 5 Text figures)

FOR THE PAST SEVERAL YEARS, we have been conducting investigations on subtidal populations of nudibranchs occurring around the island of Oahu (JOHNSON & BERTSCH, 1979; and BERTSCH & JOHNSON, 1980 a & b; 1981). We have encountered specimens of Indo-Pacific species previously unreported from the Hawaiian Islands (cf. BERTSCH & JOHNSON, 1979), and we have also collected specimens of new species of nudibranchs.

Several Hawaiian nudibranch species were erroneously identified and reported as previously named species by KAY & YOUNG (1969). RUDMAN (1978) recognized the apparent uniqueness of several of these species, and referred to them as undescribed species of *Sclerodoris*. KAY (1979: 464-465) agreed with him. However, careful examination of additional material has revealed a complex of unnamed species in several genera which require more research. We have obtained sufficient material to describe 3 of them as new species in this paper. These new species are apparently endemic to the Hawaiian Islands.

ALDISIDAE Odhner, 1939

Aldisa Bergh, 1878

Aldisa pikokai Bertsch & Johnson, spec. nov.

(Figures 1-2 and 6-8)

REFERENCES:

Halgerda rubra (not Bergh, 1905). KAY & YOUNG, 1969: 194 (in part; external anatomy of smaller specimens only); not fig. 31.

Sclerodoris sp. RUDMAN, 1978: 76 and 86 (in part, when referring to external anatomy of Kay & Young's specimen). KAY, 1979: 465 (in part); fig. 147 C.

Aldisa sp. BERTSCH & JOHNSON, 1981: 44-45 (includes color photographs).

EXTERNAL MORPHOLOGY AND COLORATION

Sizes of 3 living animals were 9.5, 11 and 14 mm long, and 6.5, 9 and 7 mm wide. An ovalish shaped dorid (Figure 6), its dorsal surface is reticulated with a series of raised ridges. Where ridges meet (often 4-5 come together) they rise into a pointed peak, like a small papilla. Minute, straight spicules (6-10 in number) protrude outward from each papilla. Viewed with a dissecting microscope at 250 x, sheets of spicules can be seen lying underneath the integument. Dorsum is rigid and slightly convex. A thin mantle margin overhangs edges of foot. Rhinophores and gills are positioned relatively far anteriorly and posteriorly,

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respectively. In a preserved specimen 14 mm long the rhinophores were 2.5 mm apart, and 3 mm from the anterior edge of the animal; the gills were about 2.5 mm from the posterior edge of the mantle. On the midline of the dorsum are 3 depressions, giving the animal a cratered appearance. These pits vary in outline (circular to ovalish), and are each surrounded by a raised rim. One pit lies just anterior to the rhinophores, the next pit is immediately posterior to the rhinophores and the third is just anterior to the gills. All three are each within 1 mm of either the rhinophores or gills. The size of these pits does not vary significantly in proportion to the size of the adult animals. In living specimens measuring 9.5, 11 and 14 mm long the diameters of the pits in each animal were: 1, 1.75, and 1.5 mm; 0.5, 1, and 1 mm; and 0.5, 2, and 1.5 mm, respectively. The pits of a preserved specimen 14 mm long were 1, 2 and 1.75 mm in diameter.

Basic body color of living animal is an orange-red with infrequent dust-like patches of cream white on the sides of the dorsum. Rhinophores are orange-red, gills cream white. Inside the pits are numerous small dark maroon-black pigmented spots (see BERTSCH & JOHNSON, 1981: 44-45).

Additional descriptions of the external anatomy (smaller specimens only) are given by KAY & YOUNG, 1969: 194, and KAY, 1979: figs. 147 C and p. 467.

RADULA:



Figure 1

Two radular teeth of *Aldisa pikokai*, approximately 400 X (specimen HB 754 B; paratype)

Buccal tube contains a multitude of elongate thin teeth (Figure 7); "dont les éléments sont aussi difficiles à compter que ceux d'une chevelure hirsute!" (PRUVOT-FOL,

1954: 268). One specimen (HB 754-B) had approximately 85 + teeth per half-row, whereas a larger specimen (HB-753-A) had about 120 teeth per half-row (with around 200 total rows). Because of the thinness and overlapping of

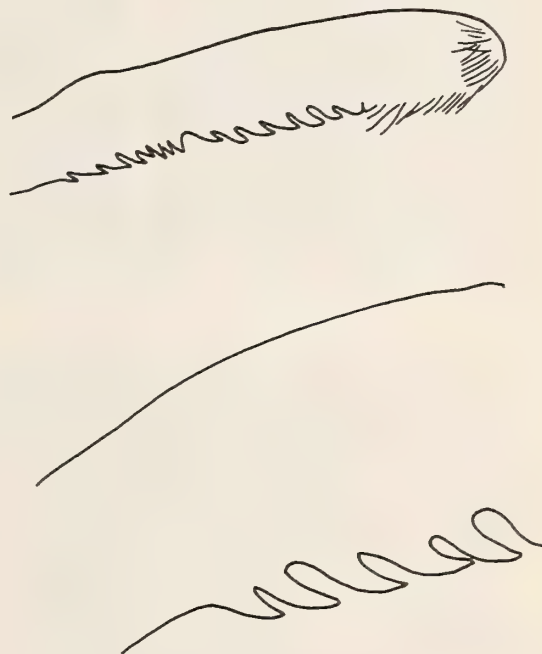


Figure 2

Close-ups of distal end of tooth, showing fine serrations. Upper tooth, approximately 2250 X, lower drawing approximately 5600 X (*Aldisa pikokai* specimen HB 754 B)

teeth, the row patterns are extremely difficult to discern. Each tooth is broadened at the base, becoming thin throughout most of its length, then widening into a flat, spatulate shape distally (Figure 1). The broader end has a series of about 18-25 small up-curved denticles (Figure 2) along one side. At the extreme distal point the serrations become very long and thin, often folding back over the tip (Figure 8).

Note added in proof;

We sent Dr. Sandra Millen (University of British Columbia, Canada) a specimen of *Aldisa pikokai*, and she graciously furnished us this description of its reproductive system:

"The ovotestis forms small oval lobules on the surface of the digestive glands. The thin hermaphroditic duct leaves above the esophagus and travels anteriorly to the saccate, u-shaped ampulla. This ampulla narrows to a short duct which branches to the prostate, to the short uterine duct and to a long duct which travels upward across the albumen gland.

"The elongate prostate is u-shaped, the non-prostatic portion of the vas deferens narrows and coils slightly, widening into a muscular portion terminating at the penis. The penis is armed with spines. The thorn-like spines, 10 μ m long, are arranged in 6 rows, of approximately 11 per row.

"The female gland has a separate nidamental opening ventral to the male-female opening. The mucus and membrane portion is highly pigmented, orange in alcohol. The granular white albumen gland is located centrally.

"The vagina is connected to a common atrium. It is long and tubular, muscular near the atrium, narrowing slightly and ending in the small, round bursa copulatrix. At this junction emerges the duct to the semi-serially arranged receptaculum seminis. Two-thirds of its length along it bifurcates, recurving to the rounded receptaculum seminis and sending off a long, thin uterine duct to enter the base of the albumen gland."

MATERIAL EXAMINED AND DISTRIBUTION:

1) Holotype. 5 m subtidal, Makua, Oahu; leg. Scott Johnson (SJ), 17 August 1978 (HB 753-A). This dissected specimen and its mounted radula have been placed in the collections of California Academy of Sciences, Department of Invertebrate Zoology, CASIZ 019702.

2) Paratype. 5 m subtidal, Makua, Oahu; leg. SJ, 30 April 1979, night scuba dive. Undissected specimen in the Malacology Department, Bernice P. Bishop Museum, Honolulu, Cat. No. 207078.

3) Paratypes. 2 specimens, 5 m subtidal, Makua, Oahu; leg. SJ, October 1978 (HB 754). Alcohol preserved specimens and

mounted radula slides, San Diego Natural History Museum, Department of Marine Invertebrates, Type Series SDNHM No. 800.

4) Additional Material. 1 specimen, 5 m subtidal, Makua, Oahu; leg. SJ, 10 May 1979, night scuba dive (HB 840); 1 specimen, 9-10 m subtidal, Pupukea, Oahu; leg. SJ, 9 July 1979, night scuba dive (HB 841); 1 specimen, 5 m subtidal, Makua, Oahu; leg. SJ, 19 September 1979, night scuba dive (HB 842); 1 specimen, 14 m subtidal, Ewa, Oahu; leg. SJ, 13 October 1979; 1 specimen, 24 m, Haleiwa Trench; leg. Hans Bertsch (HB), Judith Bertsch, and Jane Culp, 17 August 1980.

5) 1 specimen, 8 m, Puako, Hawaii; seen by SJ, 20 May 1978. 11 specimens, 2, 8 and 10 m, Puako, Hawaii; seen by SJ, 8, 9, 11, 12 and 14 August 1980.

6) More than 100 specimens have been seen while night diving at Pupukea and Makua, 1978-1980 (see Table 1).

We have temporal and bathymetric data on 134 specimens of *Aldisa pikokai*. The species is nocturnal; we observed 124 animals at night and 10 during daylight hours. Eight of the daylight-found animals were under rocks, and 1 was at the bottom of the Haleiwa Trench (the deepest specimen recorded); these situations are relatively dark habitats for the animal.

Aldisa pikokai occurs in the shallow subtidal zone. We found 32 specimens between 2-12 m deep, 1 in 14 m, and 1 in 24 m (the Haleiwa Trench specimen). The median depth at which we found specimens was 2-6 m; over 75% of the animals were collected between 2-8 m (Table 4).

TYPE LOCALITY:

Shallow subtidal cliffs off of Makua, Oahu (21°32'50" N; 153°13'32" W); Hawaiian Islands.

ETYMOLOGY:

This new species name is a combination based on the Hawaiian words *piko* (navel) and *kai* (sea), forming a genitive ending of the second declension (only one -i used

Explanation of Figures 6 to 12

Figure 6: *Aldisa pikokai*, collected at Pupukea, night diving in 10 m of water

Figure 7: Radular teeth of *Aldisa pikokai* (specimen HB 754 B); low magnification scanning electron micrograph showing the characteristically thin, elongate teeth $\times 115$

Figure 8: Distal tip of radular tooth of *Aldisa pikokai*, $\times 5600$

Figure 9: Holotype of *Sclerodoris paliensis*, photograph of living animal (HB 755)

Figure 10: SEM of anterior half of radula of *Sclerodoris paliensis* Specimen illustrated, HB 755, holotype $\times 20$

Figure 11: Posterior half of radula, left side, of *Sclerodoris paliensis* $\times 20$

Figure 12: Posterior half of radula, right side, of *Sclerodoris paliensis* $\times 20$



Figure 6



Figure 7



Figure 8

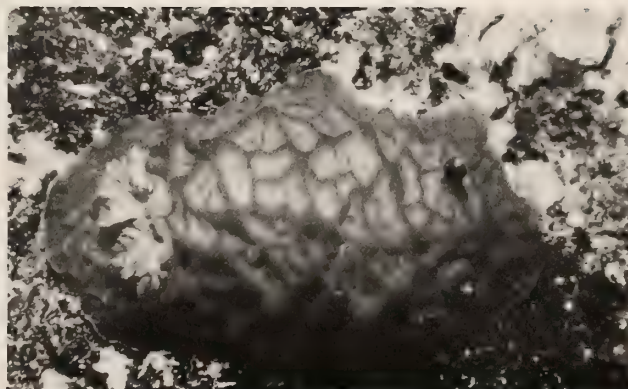


Figure 9



Figure 10

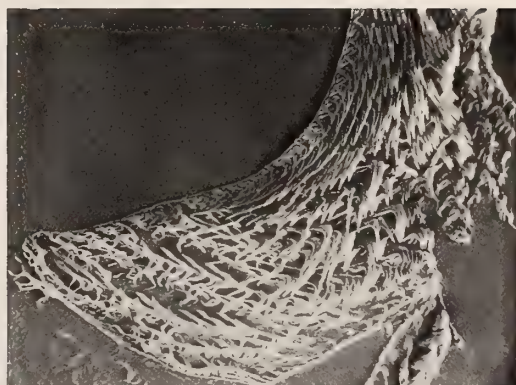


Figure 11

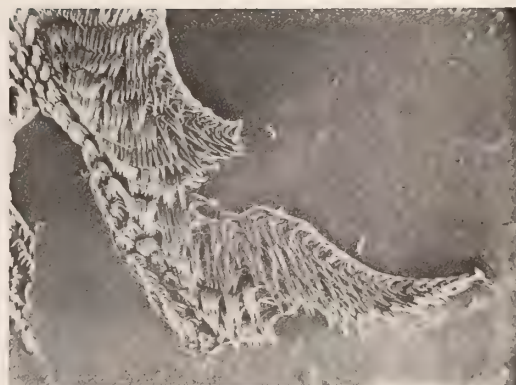


Figure 12

Table 1

Monthly occurrences of specimens of *Aldisa pikokai*, seen (not collected) at Makua and Pupukea, Oahu.

Month	Makua	Number of scuba dive searches	Pupukea	Number of scuba dive searches	Total animals	Total searches
January	8	2	—	—	8	2
February	1	1	—	—	1	1
March	9	2	1	1	10	3
April	11	3	—	—	11	3
May	—	—	7	1	7	1
June	13	2	—	—	13	2
July	12	2	4	2	16	4
August	12	2	3	2	15	4
September	18	4	—	—	18	4
October	3	1	—	—	3	1
November	—	—	—	—	—	—
December	11	3	—	—	11	3

for euphony), and meaning sea navel, in reference to the poem:

Pohaku piko Navel stone
Piko honua Earth navel

According to the traditions of the Hawaiian people, the "child's navel cord attaches him to his mother and family. He will be attached also to the place where the cord is deposited after his birth. If it is placed in the sea, he will live from the sea. If his cord is pounded firmly into the crevice of the proper stone, he will be forever a child of the land which nurtures him" (CHARLOT, 1978). The dorsal pits on *Aldisa pikokai* are reminiscent of the cupule style petroglyphs fashioned on pahoe-hoe lava flows (at Puuloa, Hawaii) in which were deposited the children's navel cords (COX & STASACK, 1970: 21-24).

DISCUSSION:

In their study of the Hawaiian dorids, KAY & YOUNG (1969: 194-195) identified 3 red nudibranch specimens as *Halgerda rubra* Bergh, 1905. RUDMAN (1978: 76) considered that these specimens were an unnamed new species of *Sclerodoris*, which opinion KAY (1979: 465) followed. Neither author examined additional specimens. However, Kay & Young's original material, collected in 1965-1966, is actually a composite of several species. Their external description and the smaller measurements were based on specimens of our new species, *Aldisa pikokai*. The internal descriptions are not referable to any material we have examined.

Species of the monotypic family Aldisidae are characterized by a highly aberrant radula, composed of fine, elongate teeth, serrated and spatulate at the distal extremity (cf. illustrations in PRUVOT-FOL, 1954: 267-269; fig. 106; MARCUS, 1961: 16; fig. 53; FERREIRA & BERTSCH, 1975: 328; figs. 11-14). The living animals tend to be small dorids (usually less than 30 mm) and colored in varying shades of yellow orange or red (BEHRENS, 1980: 50).

The dorsal surface of all previously known species of *Aldisa* is papillose, tuberculous, or verrucose. The dorsal surface textured with ridges and pits is a unique morphological feature that immediately separates *Aldisa pikokai* from the 6 known species of *Aldisa*.

This new Hawaiian species of *Aldisa* is also geographically isolated from all its congeners. *Aldisa banyulensis* Pruvot-Fol, 1951, *A. berghi* Vayssière, 1901, *A. binotata* Pruvot-Fol, 1953, and *A. zetlandica* (Alder & Hancock, 1854) occur along the North Atlantic or Mediterranean coasts (see THOMPSON & BROWN, 1976: 124; and PRUVOT-FOL, 1954: 268-269). These species are finely or grossly papillated on the dorsum, and lack any hint of the reticulated ridges seen on *Aldisa pikokai*. Moreover, *Aldisa zetlandica* is a gray-green color.

Aldisa cooperi Robilliard & Baba, 1972, occurs around the margins of the north Pacific, in Japan, northern British Columbia, Canada, Washington, and California, USA (LAMBERT, 1976). *Aldisa sanguinea* (Cooper, 1863) ranges from Coos Bay, Oregon (BELICK, 1975), to San Diego, California, and in the Gulf of California, Mexico (FERREIRA & BERTSCH, 1975: 327-328). The records of *A.*

cooperi in California (ROBILLIARD & BABA, 1972: 412) and *A. sanguinea* in Oregon suggest a sympatric and not allopatric distribution. Hence, *A. cooperi* is here given full specific status, although originally named as a subspecies. Both species can be distinguished from *A. pikokai* by their papillated notum and their patterns of black coloration (two large blotches or many small specks).

Aldisa nhatrangensis Risbec, 1956, is a synonym of *Actinocyclus japonicus* (Eliot, 1913) (KAY & YOUNG, 1969: 217).

HALGERDIDAE Odhner, 1926

Sclerodoris Eliot, 1904

Sclerodoris paliensis Bertsch & Johnson, spec. nov.

(Figures 3-4, and 9-14)

REFERENCES:

Sclerodoris sp. BERTSCH & JOHNSON, 1981: 45 (includes color photograph).

EXTERNAL MORPHOLOGY AND COLORATION:

Maximum length of living animal is about 65 mm; preserved lengths of 5 specimens were 28, 34, 37, 45 and 51 mm. Dorsal surface is evenly convex and heavily criss-crossed with anastomosing ridges. The junctures of 3-5 major ridges are further raised as prominent papillae (Figure 9). One's immediate impression on viewing this animal is of the large size of the ridges compared with the gouged-out pits between them. Rhinophores of 42 mm long animal were positioned 7 mm from the anterior edge of body, 10 mm apart (body width 22 mm).

Body coloration is a dirty yellow to yellow-orange. Some of the ridges are a darker and denser yellow. A delicate, thin white line edges the notum; some have none, while others have a lightly frosted appearance. The gills are a dirty cream color; the rhinophores are yellow basally, dusty brown in the broader area of the perfoliations, tipped in white distally (see BERTSCH & JOHNSON, 1981: 45).

INTERNAL ANATOMY:

The combined radular formula from 7 specimens is 37-44 (33-45+33-45). Table 2 gives the individual formulae. Radular teeth are simply hamate (Figures 3 and 10-12);

innermost teeth have short and strongly curved cusps, becoming progressively longer and straighter in the center of each half-row. Outermost lateral teeth are shorter and straight (Figure 13). Newly developing teeth (Figure 14) are weaker and thinner, characteristic of such teeth (BERTSCH, 1976).

Table 2

Radular formulae of *Sclerodoris paliensis*.

Specimen	Formula	Length of animal
HB 755	43 (41.0.41)	42 mm alive
HB 845	44 (33.0.33)	
HB 844 a	42 (45.0.45)	37 mm preserved
HB 844 b	41 (38.0.38)	45 mm preserved
HB 844 c	38 (36.0.36)	34 mm preserved
HB 844 d	42 (43.0.43)	51 mm preserved
HB 846	37 (37.0.37)	28 mm preserved

The newest radular teeth begin growing on the outermost portion of the most posterior tooth row. As the tooth row advances, the central and inner teeth of each half-row are formed. Thus, progressive inward growth of the developing tooth rows is mirrored in the increased number of teeth. The ultimate tooth row of one specimen had 11 teeth in the half-row (row 42, right side of radula, HB 844 A); the penultimate row (number 41) had 21 teeth in the half-row, and row 40 had 27 teeth.

The radulae of bigger specimens tend to be larger because of increased tooth size, not an increased number of rows of teeth.

The reproductive system (Figure 4) is similar to that of other species of *Sclerodoris*. There is a distinct prostate, a spermatocyst (exogenous sperm sac) attaches near the prostate and ampulla, and no accessory gland opens into the vestibule housing the genital apertures.

MATERIAL EXAMINED:

1) Holotype. 5 m subtidal, Makua, Oahu; leg. Scott Johnson, 24 August 1978, night (HB 755). This dissected specimen and its mounted radula have been placed in the collections of California Academy of Sciences, CASIZ 019700.

2) Paratype. 5 m subtidal, Makua, Oahu; leg. SJ, 10 May 1979, night (HB 846). Alcohol preserved specimen and mounted radular slide, San Diego Natural History Museum, Department of Marine Invertebrates, SDNHM T.S. 802.

3) Additional material. 1 specimen, subtidal, Makua, Oahu; leg. SJ, April 1977 (color transparency, specimen not col-

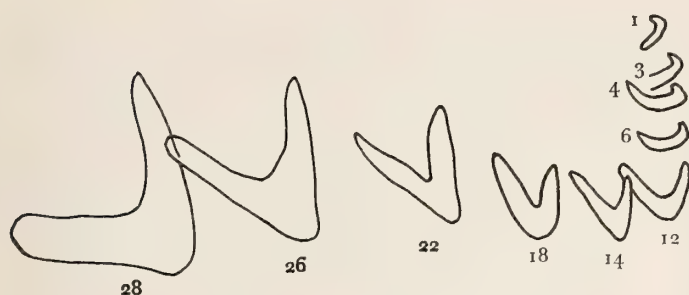


Figure 3

Radular teeth of *Sclerodoris paliensis*:

- A. Selected teeth from row 25, right side (specimen HB 845; collected in 10 m at Pupukea by S. Jazwinski, 15 March 1979); approximately 200 ×
- B. Outer 10 teeth of row 10, right side (specimen HB 845) approximately 200 ×
- C. Anomalous tooth shape (bicuspid), present in tooth 4, right side, rows 7 through 29 (specimen HB 846, paratype)

lected); 4 specimens, 5 m, Makua, Oahu; leg. SJ, 25 January 1979, night (HB 844); 1 specimen, 10 m, Pupukea, Oahu; leg. Stan Jazwinski, 15 March 1979; 1 specimen, dredged 500 feet [150 m] from sand and coral rubble bottom, due west off Pokai



Figure 4

**Sketch of reproductive system of *Sclerodoris paliensis*
(specimen HB 844 B)**

Bay; leg. Richard Salisbury, 1976 (not seen; *fide* personal communication R. Salisbury).

4) Other animals were seen by SJ, night diving at Makua, Oahu, but not collected: 2 specimens, 10 March 1978; 3 specimens, 17 April 1978; 1 specimen, 9 June 1978; 3 specimens, 8 July 1978; 4 specimens, 17 August 1978; 3 specimens, 11 September 1978; 3 specimens, 25 September 1978; 3 specimens, 20 October 1978; 5 specimens, 25 December 1978; 5 specimens, 13 April 1979; 1 specimen, 20 April 1979; 1 specimen, 30 April 1979; 2 specimens, 20 September 1979; 1 specimen, 5 December 1979; 2 specimens, 3 January 1980; 1 specimen, 29 July 1980.

5) 3 specimens seen at Puako, Hawaii, 5-10 m, 9-14 August 1980, SJ.

Sclerodoris paliensis is nocturnal; 51 (out of 52) animals were collected at night. It usually occurs in the shallow subtidal zone. Similar to *Aldisa pikokai*, the median depth at which we found specimens was 2-6 m; 75% of the animals were collected between 2-6 m (Table 4).

TYPE LOCALITY:

Shallow subtidal cliffs off of Makua, Oahu (21°32'50" N; 153°13'32" W).

ETYMOLOGY:

Based on the Hawaiian word for cliff, *pali*, the species name was chosen because the steep ridges on the animal's notum bear a resemblance to the steep cliff face characteristic of erosion of an extinct volcano in the Hawaiian Islands.

DISCUSSION:

This species apparently has not been reported previously from Hawaii nor elsewhere in the Indo-Pacific, not even as a misidentified specimen, by other workers.

RUDMAN (1978) reviewed the genus *Sclerodoris* as comprised of 8 Indo-Pacific species. One of these, *Sclerodoris* sp. A., he separated from *Halgerda rubra* under which identification KAY & YOUNG (1969) published a description of their specimens. We have shown that part of this material is actually our new species of *Aldisa*, and therefore need not be compared with *Sclerodoris paliensis*. Recently, BERTSCH (1981) has recognized one other species in this genus: the Californian-west Mexican *Sclerodoris tanya* (Marcus, 1971), the first non-Indo-Pacific *Sclerodoris* known.

Sclerodoris tuberculata Eliot, 1904, and *Sclerodoris* sp. B. (*sensu* RUDMAN, 1978: 86) both have denticles on their outermost radular teeth; these teeth are smooth in *Sclerodoris paliensis*. The outermost teeth of *Sclerodoris coriacea* Eliot, 1904, have one large cusp and a number of irregular projections, a trait not shared by *S. paliensis*; moreover the body texture of *S. coriacea* is different—with many close tubercles, and without the prominent ridging of *S. paliensis*. The enigmatic *Sclerodoris osseosa* (Kelaart, 1859), reported from Ceylon and Africa, has an indistinct dorsal ridge, with "one pit larger and more conspicuous than the others" (ELIOT, 1904: 380), traits not present in *S. paliensis* (see RUDMAN, 1978: 85-86, for a discussion of Hawaiian specimens identified as *Trippa osseosa* by KAY & YOUNG, 1969). Both *S. tuberculata* and *S. apiculata* Alder & Hancock, 1864, have an accessory gland in their reproductive system, absent in *S. paliensis*. Notal texture is also useful for specific separation: *Sclerodoris japonica* (Eliot, 1913) has a back closely covered with villous papillae; *S. tarka* Burn, 1969, and *S. apiculata* have a delicate style or filament projecting from each tubercle; *S. tanya* has a complicated texture which includes pits or holes in the walls of the main concavities and depressions. These characters do not occur in *S. paliensis*.

The genus *Peronodoris* Bergh, 1904, has been variously synonymized with *Sclerodoris* (THIELE, 1931; ALLAN, 1947), considered a distinct genus (MARCUS & MARCUS, 1970) or thought in need of further material before a decision could be made (RUDMAN, 1978). Without proffering an opinion regarding the status of *Peronodoris*, we feel that our new species should be compared with the 3 species placed within that genus because of their distinct notal ridging and possible close affinities with *Sclerodoris*. The differences can be summarized succinctly: *Peronodoris*

cancellata Bergh, 1904, has no prostate; and *P. denticulata* Eliot, 1908, and *P. rehderi* Marcus & Marcus, 1970, have teeth with denticles.

Halgerda Bergh, 1880

Halgerda terramtuensis Bertsch & Johnson, spec. nov.

(Figures 5, and 15-18)

REFERENCES:

- Halgerda* sp. cf. *graphica* (Not Basedow & Hedley, 1905.) KAY & YOUNG, 1969: 193-194; figs. 28 and 30. RUDMAN, 1978: 84. KAY, 1979: 474; fig. 147 E.
Halgerda grafica. BERTSCH in SUMICH, 1980: plt. 6-D (color photograph).
Halgerda sp. BERTSCH & JOHNSON, 1981: 46-47 (includes color photographs).

EXTERNAL MORPHOLOGY AND COLORATION:

Sizes of 26 living animals ranged from 15-50 mm in total length ($\bar{X} = 29.9$ mm); over $\frac{2}{3}$ s of the animals measured 25-50 mm. This is a much wider range of size than the 25-30 mm reported by KAY & YOUNG (1969). This oval shaped dorid has a convexly inflated dorsal region (Figure 15). Its body is a firm, gelatinous, smooth texture, with harder pustules scattered over the notum. Mantle margins are thin, at times appearing slightly scalloped or crenulate. Body is a translucent white (viscera visible through integument as darker areas), and the notum is covered with a network of yellow-gold lines, forming irregular polyhedrons. White pustules occur at the juncture of the lines. Mantle is margined with a complete yellow-gold edging. The long slender rhinophores and gills (2 branchiae which further divide) are white with black spotting (see BERTSCH & JOHNSON, 1981: 46-47).

INTERNAL ANATOMY:

The combined radular formula from 5 specimens (including Kay & Young's) is 55-62 (45-61 · 0 · 45-61). Individual formulae are listed in Table 3. The radular teeth have smooth, hamate cusps, increasing in length in the middle of each half-row (Figure 16 of this paper; see also KAY & YOUNG, 1969: figs. 28-B). Outermost teeth decrease to nearly scythe-like blades (Figure 17). Newly developing teeth are exceedingly thin (Figure 18). Some of the central teeth (Figure 5) are longer, thinner and straighter than

Table 3

Radular formulae of *Halgerda terramtuensis*.

Specimen	Formula	Length of animal
HB 702 (SEM)	59 (45.0.45)	21 mm preserved
HB 727	61 (59.0.59)	42 mm preserved
HB 742 a	51 (50.0.50)	18 mm preserved
HB 855 a	62 (61.0.61)	32 mm preserved
Kay & Young (1969)	55 (56.0.56)	30 mm

the thicker shapes illustrated by Kay & Young. This variation is certainly not considered a significant difference. The major component of radular size variation between larger and smaller specimens appears to be size of teeth and not number of rows.

Reproductive system has been described and figured by KAY & YOUNG (1969: 193-194; fig. 28-A).



Figure 5

Tooth of *Halgerda terramtuensis*, dissected from near the middle of row 15, left side (specimen HB 727, paratype)

MATERIAL EXAMINED AND DISTRIBUTION

1) Holotype. 22.9 m, subtidal, about 1-2 km offshore from Waikiki, Oahu; leg. Hans Bertsch, 16 September 1978 (HB 702). This dissected specimen and its mounted radula have been placed in the collections of California Academy of Sciences, Department of Invertebrate Zoology, CASIZ 019701.

2) Paratype. 15.2 m, off Halona Blowhole-Lanai Lookout Cliffs, Oahu; leg. HB & SJ, 26 September 1978 (HB 727). Alco-

hol preserved specimen and mounted radular slide, San Diego Natural History Museum, Department of Marine Invertebrates, SDNHM T.S. 804.

3) Additional material. (Mostly seen and photographed *in situ*, not collected). 2 specimens, 21.3 m, boat dive off Makaha, Oahu; HB & Judith Bertsch, 17 September 1978; 2 specimens, 15.2 m, Pupukea, Oahu; HB & SJ, 21 September 1978; 1 specimen, 16.8 m, Makua Ledge, Oahu; HB & SJ, 2 October 1978; 1 specimen, 35 m, off Lahi Lahi Point, Makaha, Oahu; HB & Judith Bertsch, 10 December 1978.

6 specimens, 6 m, Three Tables, Oahu; HB & Rosemary Dorostkar, 30 June 1979; 2 specimens, 15 and 25 mm in length, 12 m, Makua Ledge, Oahu; HB & Scott Greenberg, 5 July 1979; 2 specimens, 6 m, Three Tables, Oahu; HB & Jane Kent, 6 July 1979; 2 specimens, 20 mm long, 12 m, Makua Ledge, Oahu; HB, Jane Kent, and Rebecca McElroy, 11 July 1979; 2 specimens, 15 and 25 mm long, 22.9 and 20 m, Haleiwa Trench, Oahu; HB & Scott Greenberg, 12 July 1979; 2 specimens, 17 and 25 mm long, 18.3 m, boat dive off Waikiki, Oahu; HB, Rebecca McElroy, Jane Kent, and Ed Baughman, 15 July 1979.

1 specimen, 30 mm long, 10.7 m, Pupukea, Oahu; HB, 21 June 1980; 1 specimen, 32 mm long, 4.6 m, Nanakuli Beach Park, Oahu; HB & Cathie Diekmann, 29 June 1980; 1 specimen, 30 mm long, 12 m, Three Tables, Oahu; HB, Cathie Diekmann & Caroline Boeckman, 3 July 1980; 2 specimens 45 and 22 mm long, 18.3 and 16.8 m, Haleiwa Trench, Oahu; HB, Judith Bertsch, and Dan Gieschen, 4 July 1980; 4 specimens, 38, 40 and 40 mm long (9.1 m) and 50 mm long (7.6 m), on roof of lava tube, Three Tables, Oahu; HB & Judith Bertsch, 5 July 1980; 1 specimen, 40 mm long, 12 m, Pupukea, Oahu; HB, Dodie Anderson, and Cathie Diekmann, 8 July 1980; 3 specimens, 23 and 28 mm (12 m) and 20 mm long (12.8 m), Makua Ledge, Oahu; HB & Dodie Anderson, 15 July 1980; 3 specimens, 36, 30 and 30 mm long, 12.5, 12, and 12.8 m, the cave west of Makua, Oahu; HB & Jane Culp, 20 July 1980; 2 specimens, 25 mm long, 20.7 and 15.2 m, boat dive off Makaha, Oahu; HB & Judith Bertsch, 27 July 1980; 1 specimen, 36 mm long, 6.7 m, Three Tables, Oahu; HB & Jane Culp, 15 August 1980; 1 specimen, 35 mm long, 9.1 m, Pupukea, Oahu; HB & Judith Bertsch, 24 August 1980.

1 specimen, 54 mm long, subtidal, Kona, Hawaii; leg. A. J. Ferreira, June 1973.

KAY & YOUNG (1969: 194) found only 4 specimens of this species (2 were collected from 13 m depth) during over 4 years of regular monthly littoral collections. Our 3 years of scuba diving have yielded over 100 specimens of *Halgerda terramtuensis*. Only 60% of the animals were seen between 2-6 m deep (Table 4).

In an earlier work studying Chromodorididae nudibranchs, we have contrasted the results of our subtidal field work to KAY & YOUNG's (1969) intertidal data (see BERTSCH & JOHNSON, 1980). We have found definite zonation preferences among the species of chromodorids for the intertidal or subtidal regions and different bathymetric ranges within the subtidal zone. In a similar fashion, there are distinct habitat and niche differences among

Table 4

Bathymetric distribution of *Aldisa pikokai*, *Sclerodoris paliensis*, and *Halgerda terramtuentis*. The large numbers of animals seen in the 2-6 m depth range partially reflects intensive observations by SJ at this depth; however, the relative proportions between the different depth occurrences and between the species indicate that *H. terramtuentis* is more common deeper.

Depth in meters	Number of animals		
	<i>Aldisa pikokai</i>	<i>Sclerodoris paliensis</i>	<i>Halgerda terramtuentis</i>
0 - 4	1	—	1
(2 - 6)	84	40	66
5 - 8	19	9	10
9 - 12	28	2	18
13 - 16	1	—	6
17 - 20	—	—	5
21 - 24	1	—	4
25 +	—	1 (dredged)	1
Total animals	134	52	111
Nocturnal (observed while night diving)	124	51	35 (all from 2 - 6 m)

the 3 species described in this paper. *Aldisa pikokai* has a remarkably different radular tooth morphology from both *Sclerodoris paliensis* and *Halgerda terramtuentis*. Our new species of *Aldisa* and *Sclerodoris* both occur more commonly in the shallow subtidal area and are nocturnal. The new *Halgerda* occurs more frequently in deeper water and is both diurnal and nocturnal.

TYPE LOCALITY:

About 1-2 km offshore from Waikiki Beach, Oahu (21°16'30" N; 157°50'30" W).

ETYMOLOGY:

The species name is an interpretive Latin translation for an Earthwatch team member (literally, "of the one

looking at the earth with care"), to acknowledge the support and help given our research by the volunteer Earthwatch expeditions "Hawaii's Colorful Mollusks," during the summers of 1978, 1979, and 1980.

DISCUSSION:

Halgerda terramtuentis needs to be clearly distinguished from *Halgerda graphica* Basedow & Hedley, 1905. The radula is similar, and cannot be distinguished by meristic characters. The teeth of both species have simple hamate cusps, but Basedow & Hedley's illustrations of the Australian species indicate thinner teeth with a weaker base than Kay & Young and we have found in the Hawaiian species. The coloration is significantly different and immediately reliable for specific determination. *Hal-*

Explanation of Figures 13 to 18

Figure 13: Close-up SEM of anterior-most 4 rows of radular teeth of *Sclerodoris paliensis* (upper right hand portion of Figure 10)

× 110

Figure 14: Posterior-most rows of developing radular teeth of *Sclerodoris paliensis* (enlargement of lower center of Figure 11)

× 50

Figure 15: *Halgerda terramtuentis* photographed crawling at 9 m depth, Makua, in a strong current (2 October 1978). This illustration

appeared as a color photograph in SUMICH, 1980: pl. 6-D
Figure 16: Radula of *Halgerda terramtuentis* (HB 702); SEM of posterior $\frac{2}{3}$ of radula, showing developing rows and fully formed teeth

× 60

Figure 17: Outermost lateral teeth of *Halgerda terramtuentis* (enlargement of lower center of Figure 16)

× 300

Figure 18: Newly developing teeth of *Halgerda terramtuentis* (enlargement of upper left hand quadrant, Figure 16)

× 300



Figure 13



Figure 14



Figure 15



Figure 16



Figure 17



Figure 18

gerda graphica has a distinct longitudinal yellow-orange line along the center of the dorsum, quadrilateral yellow-orange markings which enclose similarly colored curves and lines and black dots, irregular large and small black spots underneath the mantle, small rhinophores brown distally and white basally, and six small black gills. *Halgerda terramtuensis* lacks the longitudinal dorsal line, yellow-orange curves and lines within the polyhedral markings (all the yellow-orange lines are connected with each other in a tight network), the black dorsal dots, and the black spots on the underside of the mantle. The long thin rhinophores of the new species are white with black maculations, and the 2 long, complexly-branching gills are also white with black maculations. Our new species also has clear white pustules at the junctures of some of the lines in the yellow-orange network. We have seen over 100 specimens (many not recorded in this paper), from the shallow subtidal zone to 35 m deep (Basedow & Hedley's specimens were dredged from 20 fathoms, *i.e.*, 36.6 m, not the 240 m reported by KAY & YOUNG, 1969: 194). All *H. terramtuensis* specimens consistently had all 7 characteristics, regardless of their depth of occurrence. The ranges of variation of the two species do not overlap.

Most species of *Halgerda* tend to have a whitish background coloration with yellow-orange ridges and dark spots (RUDMAN, 1978). *Halgerda terramtuensis* is one of the few without dark spots or markings on the notum. Coloration differences readily separate this new species from the previously named species. *Halgerda wasinensis* Eliot, 1904, has a dark brown mantle, becoming whitish peripherally, with dark brown spots in the white area. *Halgerda willeyi* Eliot, 1904, has a complex texture of high golden yellow ridges, with very dark purple-brown streaks between the ridges. Between the apricot yellow ridges of *Halgerda tessellata* (Bergh, 1880) are depressed regions dark purple-brown with yellow spots. *Halgerda punctata* Farran, 1905, is white with dark purple spots around the edge of the mantle. The recently named *Halgerda carlsoni* Rudman, 1978, has a mammillate appearance, with bright red-tipped conspicuous tubercles. *Halgerda elegans* Bergh, 1905, has black lines around the periphery of the mantle, and *Halgerda rubicunda* Baba, 1949, is red (or orangish). Unique to *Halgerda aurantio-maculata* (Allan, 1932) are a row of large elongated pointed fleshy protuberances down the center of the dorsum, a dorsal median ridge, and large irregular-sized rich orange yellow oval spots.

Most radulae of *Sclerodoris* and *Halgerda* have a similar formula in the range of 40-65 (35-65 · 0 · 35-65). Radular differences, therefore, must be evaluated carefully if

used for taxonomic purposes. Within both genera occur species whose teeth exhibit clearly contrasting morphological differences. Six species of *Halgerda* can be distinguished from *H. terramtuensis* on the basis of radular characteristics. *Halgerda elegans*, *H. rubicunda*, *H. wasinensis*, *H. tessellata*, *H. formosa* Bergh, 1880, and *H. xishaensis* Lin Guangyu, 1975, all have denticulate or pectinate outermost lateral teeth. The teeth of *H. terramtuensis* are all smooth.

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The Genus *Janolus*
(Nudibranchia : Arminacea)
from the Pacific Coast of North America,
with a Reinstatement of *Janolus fuscus* O'Donoghue, 1924

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(11 Text figures)

INTRODUCTION

THE SYSTEMATICS of the Janolid nudibranchs of the Pacific coast of North America has been historically riddled with confusion, although only one described species, *Janolus barbarensis* (Cooper, 1863) has been recognized for the last 15 years.

COOPER (1863) described *Aeolis barbarensis* from Santa Barbara, California. COCKERELL & ELIOT (1905) subsequently described *Janolus coeruleopictus* based on two specimens collected from San Pedro, California. In his review of the systematics of the Janolidae (as Janidae) O'DONOGHUE (1922) suggested that *Aeolis barbarensis* and *J. coeruleopictus* are conspecific, with the former having priority. In 1924 O'DONOGHUE described another species, *Janolus fuscus*, from Galiano Island, British Columbia. He stated that *J. fuscus* differs from *J. barbarensis* in its coloration and by the presence of prominent denticles on the masticatory border of the jaw which were described as being absent in *J. barbarensis* (COCKERELL & ELIOT, 1905 as *J. coeruleopictus*). JOHNSON & SNOOK (1927) employed the name *Antiopella aureocincta* in their discussion of the nudibranchs of the California coast. The name was supplied by F. M. MacFarland for a species he intended to describe. MACGINITIE & MACGINITIE (1949) also used this manuscript name of MacFarland's although they misspelled it as *A. aureotincta*. STEINBERG (1963) attempted to resolve the status of the California species and considered *A. aureocincta* Johnson and Snook, 1927 and *A. aureotincta* MacGinitie and MacGinitie, 1949 as *nomina dubia*. STEINBERG (1963) stated that further study was required to resolve questions about the status of

Janolus barbarensis (as *Antiopella*) and *J. fuscus*, but in 1966 considered the two species as being synonymous. In MACFARLAND'S (1966) posthumous monograph of the California opisthobranchs, he described *A. aureocincta* and noted color variations identical to those described for *J. fuscus* and *J. barbarensis*. SPHON & LANCE (1968) and ROLLER (1970) considered *A. aureocincta* as a junior synonym of *J. barbarensis* (as *Antiopella*). All subsequent authors with the exception of ROBILLIARD (1971), LAMBERT (1976) and ROBILLIARD & BARR (1978) have considered *J. fuscus* as a junior synonym of *J. barbarensis*.

In a recent review of the Janolidae (GOSLINER, 1981), *Antiopella* Hoyle, 1902, was regarded as a junior synonym of *Janolus* Bergh, 1884. In assessing the validity of species of *Janolus* it became apparent that a comparative study of specimens attributable to *Janolus barbarensis* and *J. fuscus* was required to resolve questions of their taxonomic status. Since then I have been able to obtain specimens of both taxa. Their comparative morphology and discussion of their taxonomic status form the basis for this study.

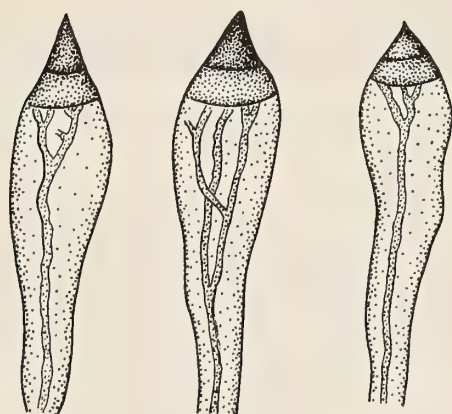
DESCRIPTION

Janolus barbarensis (Cooper, 1863)

- Aeolis barbarensis* COOPER, 1863: 59
Antiopella coeruleopictus COCKERELL & ELIOT, 1905; O'DONOGHUE, 1922
Antiopella aureocincta JOHNSON & SNOOK, 1927; STEINBERG, 1963, *nomen dubium*
Antiopella aureotincta MACGINITIE & MACGINITIE, 1949; STEINBERG, 1963, *nomen dubium*
Antiopella aureocincta MACFARLAND, 1966, in part
Janolus barbarensis (Cooper 1863); O'DONOGHUE, 1922

Material: Two specimens were collected by David Behrens of Los Osos, California from Morro Bay, California on April 18, 1978.

External Morphology: The preserved animals are approximately 15 and 20 mm long. The rhinophores are smooth basally with 20-24 perfoliations on the distal half. The inter-rhinophoral crest is rectangular, moderately convoluted. The cerata are arranged in about 20 rows on either side of the body, with 3-5 cerata per row. The cerata are smooth externally. Within each ceras (Figure 1)



1.0 mm

Figure 1

Janolus barbarensis (Cooper, 1863). Three cerata showing branching of digestive gland

the digestive gland branches irregularly. The head is rounded with a pair of short, blunt, slightly flattened oral tentacles. The anterior border of the foot is transversely grooved. The gonopores are situated laterally, just ventral to the notum on the right side of the body, near the middle of the length of the animal. The nephroproct is posterior to the gonopores. The mid-dorsal anus lies near the posterior limit of the notum.

The living animals are translucent white, often almost transparent. The inter-rhinophoral crest is red-orange. The brown pigment of the digestive gland is visible within the cerata but not within the notum. The ceratal surface bears a gold, subapical band and a blue apical band. The perfoliate portion of the rhinophores bears a lemon yellow band of pigment followed by an apical band of blue.

Digestive System: The buccal mass is large and muscular. At its anterior end, surrounding the mouth, are numerous small oral glands. The jaws (Figure 2) are strong with 7-9 denticles along the masticatory border. The radula (Figures 3, 4) has a formula of $21 \times 33.1.33$. The rachidian teeth are narrow without lateral denticles. The inner laterals possess up to 6 irregular denticles. The remaining laterals are entirely smooth, with the longest teeth being found at the outer $1/3$ of the radula. The



1.0 mm

Figure 2

Janolus barbarensis (Cooper, 1863). Jaw

largest teeth may reach $400 \mu\text{m}$ in length. The esophagus is short and expands into the corrugated anterior portion of the stomach. Large dendritic salivary glands are present on either side of stomach and enter the buccal mass ventrally. The stomach gives rise to 3 major branches of the digestive gland, as described for *Janolus capensis* and

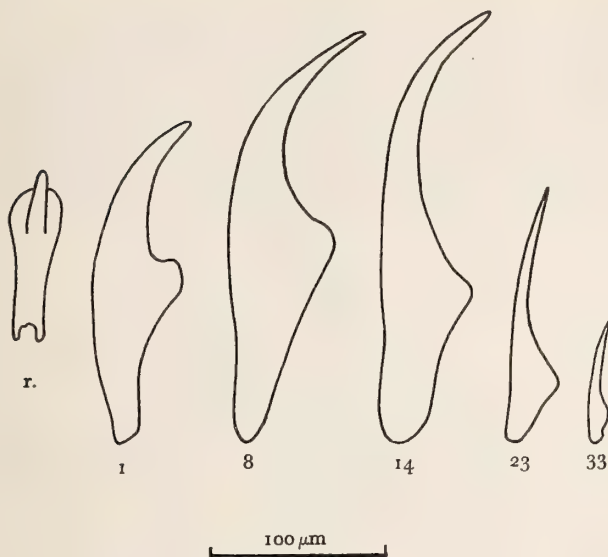


Figure 3

Janolus barbarensis (Cooper, 1863). Rachidian tooth, 1st, 8th, 14th, 23rd, 33rd lateral teeth



Figure 4

Janolus barbarensis (Cooper, 1863). Scanning electron micrograph of radula showing rachidian and inner lateral teeth. Scale: 30 μm between squares

J. longidentatus (GOSLINER, 1981). The intestine goes out from the postero-dorsal portion of the stomach and ends at the mid-dorsal anus. There is a large anal gland around the anus.

Central Nervous System: The central nervous system is essentially identical with that described for *Janolus longidentatus* (GOSLINER, 1981). The paired cerebral and pleural ganglia are well separated. The pedal ganglia are separated by a commissure of moderate length. The only noticeable difference is that the optic ganglia are much shorter in *Janolus barbarensis* than in *J. longidentatus*.

Reproductive System (Figure 5): The saccate or slightly convoluted ampulla narrows at the bifurcation of the ovi-

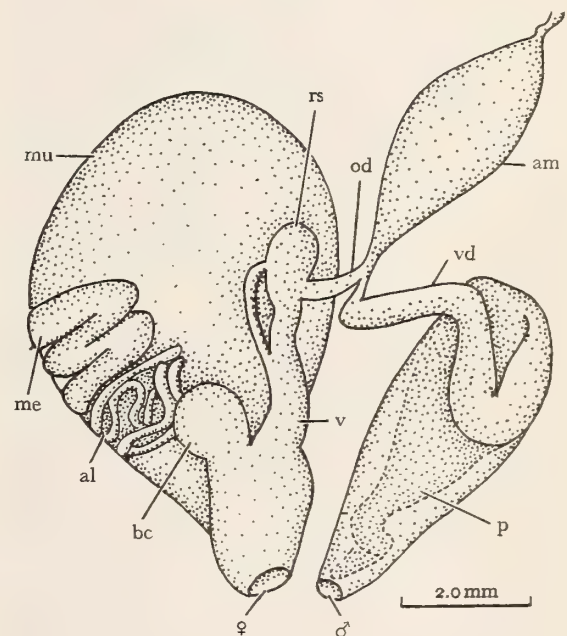


Figure 5

Janolus barbarensis (Cooper, 1863). Reproductive system.

al - albumen gland; am - ampulla; bc - bursa copulatrix
me - membrane gland; mu - mucous gland; od - oviduct
p - penis; rs - receptaculum seminis; v - vagina
vd - vas deferens; ♀ - female atrium; ♂ - male gonopore

duct and vas deferens. The vas deferens is thick and muscular throughout with few convolutions. The unarmed penis is large and muscular, thickest near the middle. The oviduct which is embedded between the lobes of the mucous gland, is muscular throughout its length and ex-

pands into a serial receptaculum seminis. A secondary duct which connects the receptaculum with the distal oviduct may be present or absent. The oviduct continues to the muscular female atrium. A spherical, thin walled bursa copulatrix enters the female atrium near its juncture with the oviduct. The albumen, membrane and mucous glands exit into the female atrium near the oviduct.

Janolus fuscus O'Donoghue, 1924

Janolus fuscus O'DONOGHUE, 1924: 16; pl. 2 (figs. 18-20)
Antiopella aureocincta MACFARLAND, 1966; in part

Material: Two specimens from the northern end of Galiano Island, Straits of Georgia, British Columbia, were collected by Sandra Millen of the University of British Columbia. Galiano Island is the type locality of *Janolus fuscus*. Mr. William Jaeckle of Humboldt State University provided 2 specimens collected from the small boat harbor at Eureka, California on 19 March, 1981 and one specimen from Abalone Beach, Humboldt County, California collected on 12 April, 1981. Additional specimens were collected by the author from San Francisco Bay and from Duxbury Reef, Marin County, California.

External Morphology: The preserved specimens are 18-25 mm in length. The rhinophores are smooth basally with 20-27 lamellae on the perfoliate, distal half. The inter-rhinophoral crest is rectangular, moderately convoluted. The cerata are arranged in 20 diagonal rows per side, with 3-7 cerata per row. The cerata are smooth, conical and somewhat inflated. Within each ceras (Figure 6) the digestive gland remains unbranched. A short, slightly flattened oral tentacle is found on either side of the rounded head. The anterior border of the foot is transversely grooved. The gonopores are situated near the middle of the right side of the body while the nephroproct is situated slightly more posteriorly. The anus is near the posterior margin of the notum.

The living animals have a translucent white ground color. On the inter-rhinophoral crest and extending posteriorly to about the midlength of the body is an irregular line of red-brown. The brown pigment of the digestive gland is visible within the translucent notum and cerata. An opaque white line runs down the center of the foot. The ceratal surface bears a subapical band of yellow and an apical band of opaque white. The rhinophores are pink in the perfoliate portion with an opaque white apex.

Digestive System: The buccal mass is large and muscular. Numerous small oral glands surround the anterior



Figure 6

Janolus fuscus O'Donoghue, 1924. Ceras showing undivided digestive gland

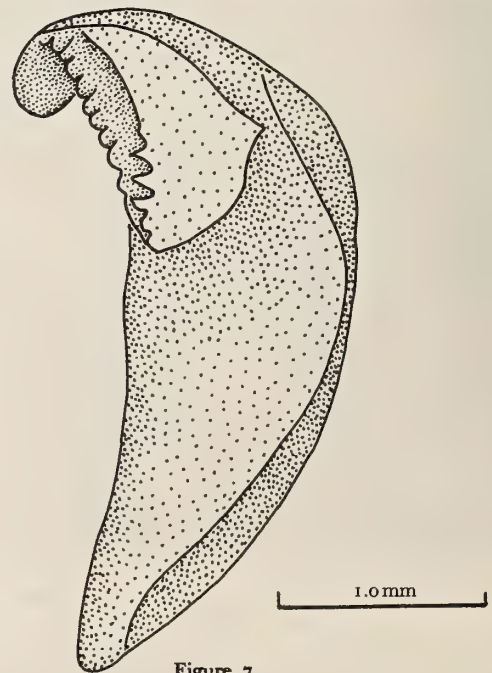


Figure 7

Janolus fuscus O'Donoghue, 1924. Jaw

portion of the buccal mass near the mouth. There are 10-13 large denticles on the masticatory border of the strong jaw (Figure 7). The radula (Figures 8, 9) has a formula of 16-25 x 24.1.24. The rachidian teeth are broad with 9-16 irregular denticles on either side of the base and central cusp. The first 1-5 lateral teeth bear 4-15 denticles on their inner margin. The remaining lateral

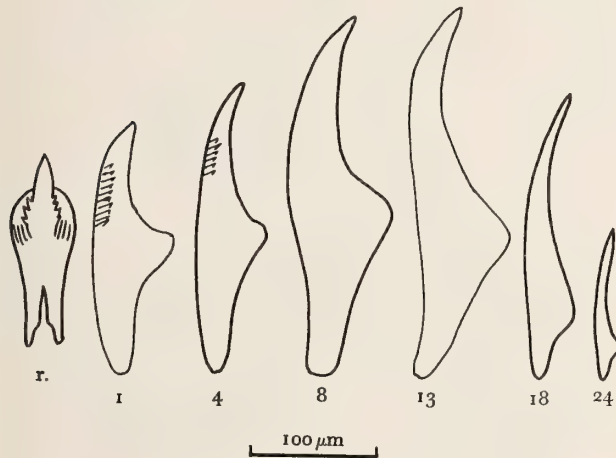


Figure 8

Janolus fuscus O'Donoghue, 1924. Rachidian tooth, 1st, 4th, 8th, 13th, 18th, 24th lateral teeth



Figure 9

Janolus fuscus O'Donoghue, 1924. Scanning electron micrograph of radula showing rachidian and inner lateral teeth. Scale: 30 μm between squares

teeth are smooth and increase in size until about to $\frac{1}{2}$ of the breadth of the half row and then diminish. The largest teeth are 300 μm long. The esophagus is short and expands into the saccate stomach. Immediately ventral to the esophagus is a large oral gland which empties ventrally into buccal mass (Figure 10). The stomach gives rise to three major branches of the digestive gland. The intestine emerges from the postero-dorsal portion of the stomach and ends at the mid-dorsal anus, which lacks anal glands.

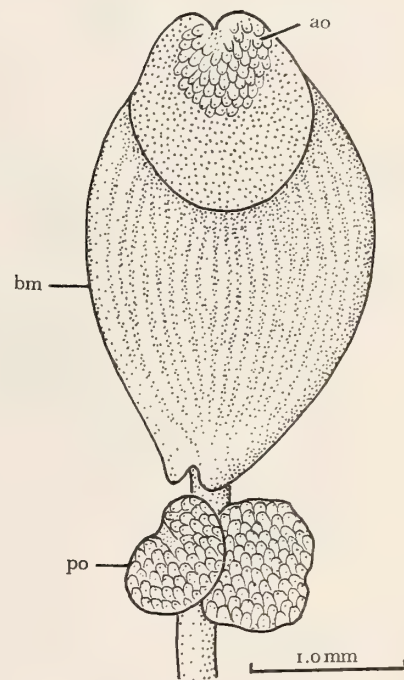


Figure 10

Janolus fuscus O'Donoghue, 1924. Buccal region.

ao - anterior oral glands; bm - buccal mass;
po - posterior oral gland

Central Nervous System: The arrangement of ganglia is identical with that found in *Janolus barbarensis* with well separated cerebral and pleural ganglia and short optic nerves.

Reproductive System (Figure 11): The ampulla is slightly convoluted and narrows into an elongate post ampullary duct. The post ampullary duct bifurcates into the oviduct and vas deferens. The vas deferens is highly convoluted and prostatic for most of its length. There is

DISCUSSION

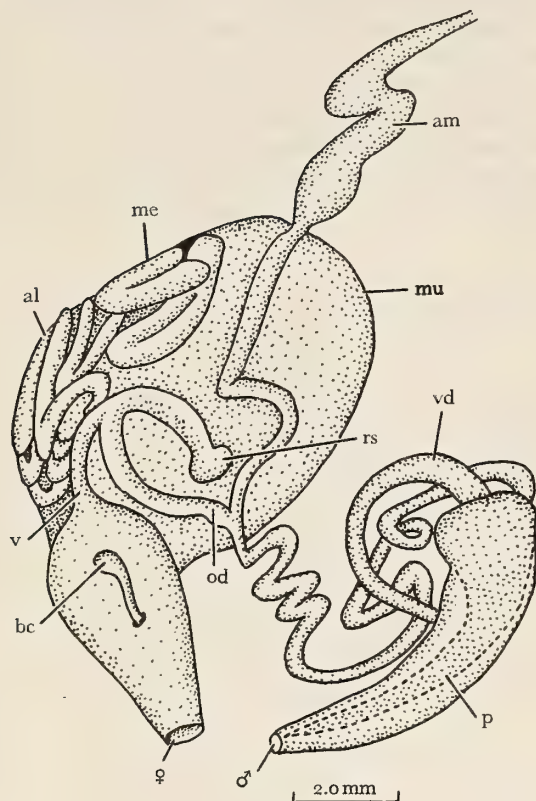


Figure 11

Janolus fuscus O'Donoghue, 1924. Reproductive system.

al - albumen gland; am - ampulla; bc - bursa copulatrix
me - membrane gland; mu - mucous gland; od - oviduct
p - penis; rs - receptaculum seminis; v - vagina
vd - vas deferens; ♀ - female atrium; ♂ - male gonopore

a short ejaculatory segment immediately proximal to the entry of the vas deferens into the penis. The unarmed penis is conical, thickened posteriorly. The narrow oviduct is embedded in the mucus gland and branches to an elongate semi-serial receptaculum seminis. The oviduct then continues distally and expands into the large female atrium. Also entering the female atrium are a pyriform bursa copulatrix and the three portions of the female gland mass, the albumen, membrane and mucous glands.

The morphology of *Janolus fuscus* O'Donoghue 1924 is poorly known. O'DONOGHUE (1924) described the external morphology and radula. MACFARLAND (1966) described *Antiopella aureocincta* and included a northern form which agrees with *Janolus fuscus* and a southern form which is clearly *J. barbarensis*. While it is not entirely clear which portions of the descriptions apply to which species, plt. 57 illustrates both species. His figs. 1 and 3 are clearly of *J. fuscus* while the cerata of *J. barbarensis* are illustrated in fig. 4. The illustrations of the reproductive system (plt. 64, figs. 11-15) are presumed to be of *J. fuscus* as there is a highly convoluted, prostatic vas deferens and conical penis. MacFarland's description differs from the present study in several significant aspects. The additional duct which connects the ampulla to the distal portion of the vas deferens, via a lobed sac, was not observed in the present material. The receptaculum seminis and bursa copulatrix were not observed by MacFarland but are present in our material.

The morphology of *Janolus barbarensis* (Cooper, 1863) is also poorly known. Cooper described only the external anatomy. COCKERELL & ELIOT (1905, as *J. coeruleopictus*) superficially described the external morphology, jaws, radula and penis. They noted that the masticatory border of the jaws was devoid of denticles. This observation is contradicted by the material examined in the present study. MACFARLAND (1966 in part, as *A. aureocincta*) illustrated the cerata of *J. barbarensis*.

Janolus fuscus O'Donoghue, 1924 differs from *Janolus barbarensis* (Cooper, 1863) in several consistent and significant regards. Externally, the two species can be distinguished by their coloration. *Janolus fuscus* has a red-brown mid-dorsal stripe on the anterior half of the animal, which is never present in *J. barbarensis*. The brown digestive gland of *J. fuscus* is visible within the cerata and in the notum, while in *J. barbarensis* it is only evident in the cerata. The cerata of *J. fuscus* have an opaque white apex, while the apices in *J. barbarensis* are blue. The rhinophores of *J. fuscus* are pink with an opaque white apex, while they are yellow and blue in *J. barbarensis*. In *J. fuscus* the digestive gland ducts within the cerata are unbranched, while in *J. barbarensis* there are several irregular divisions. The cerata of *J. barbarensis* are often more inflated than those of *J. fuscus*.

Table 1

Morphological Comparison of *Janolus barbarensis* and *Janolus fuscus*.

	Color	Ceratal ducts	Jaws	Radula	Anal glands	Oral glands	Receptaculum seminis	Bursa copulatrix	Vas deferens
<i>Janolus barbarensis</i>	translucent white; cerata with sub-apical gold band and blue apex	irregularly branched	7-9 denticles	rachidian teeth smooth	present	small, anterior	short, spherical, serial	large, saccate	short, muscular
<i>Janolus fuscus</i>	translucent white, with mid-dorsal red-brown lines; cerata with sub-apical yellow and apical white bands	un-branched	10-13 denticles	rachidian teeth denticulate	absent	small, anterior; large posterior	elongate, semi-serial	small, pyriform	elongate, convoluted, prostatic

Several features of the digestive system serve as important distinguishing characters for the two species. A large oral gland lies ventral to the esophagus in *Janolus fuscus* but is absent in *J. barbarensis*. *Janolus barbarensis* has a large anal gland around the posterior portion of the intestine which is absent in *J. fuscus*. There appear to be fewer denticles on the jaw of *J. barbarensis*.

There are radular differences which have been observed between the two species but not enough specimens have been studied to insure that these differences are consistent between *J. barbarensis* and *J. fuscus*.

The anatomy of the central nervous system is consistent between *Janolus fuscus* and *J. barbarensis*. However, the morphology of the reproductive systems differs significantly.

In *Janolus fuscus* most of the vas deferens consists of a highly convoluted, glandular prostatic portion. In *J. barbarensis* the vas deferens is much shorter and consists only of a muscular ejaculatory duct. The penial papilla of *J. fuscus* is conical, while in *J. barbarensis* it is ovate. The receptaculum seminis is serial in *J. barbarensis* and semi-serial in *J. fuscus*. *Janolus barbarensis* has a large saccate bursa copulatrix, while it is small and pyriform in *J. fuscus*. There appear to be consistent differences in the external morphology, coloration, digestive system and reproductive system which warrant the specific separation of *Janolus fuscus* O'Donoghue, 1924 from *J. barbarensis* (Cooper, 1863). These differences are summarized in Table 1. A third species of janolid has been collected from San Diego, California and was depicted by BEHRENS (1980, fig. 152). It has papillate cerata and is readily distinguishable from *J. fuscus* and *J. barbarensis*. It most closely resembles *J. hyalinus* (Alder & Hancock, 1854) and *Janolus comis* Marcus, 1955.

ACKNOWLEDGMENTS

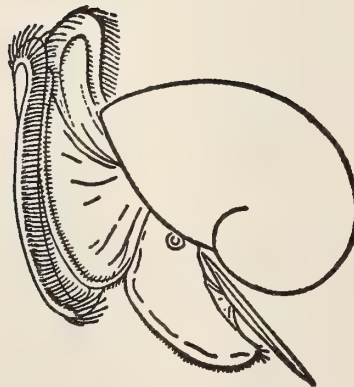
I thank Sandra Millen (University of British Columbia), David Behrens (Los Osos, California) and William Jaeckle (Humboldt State University) for providing specimens. Dr. Eveline Marcus (University of São Paulo, Brazil) critically read the manuscript and provided valuable comments.

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The Temporal Structure of Behavioral Interactions in *Hermisenda crassicornis*

(Opisthobranchia)

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(2 Text figures)

INDIVIDUALS OF THE EOLID NUDIBRANCH, *Hermisenda crassicornis* (Eschscholtz, 1831) engage in aggressive interactions with conspecifics. ZACK (1975) described the sequential structure of these interactions in detail but provided little information on their temporal structure other than overall durations. The purpose of this report is to present additional, more detailed temporal information on these interactions to add to the description of them. These interactions take on several forms that may be placed in a series graded according to the behavior patterns displayed by the participants (ZACK, 1975). At the lowest level (Zack's level Ia) two animals meet, contact one another briefly, and then move apart. In the most intense and lengthy interactions (Zack's level IIIb), two animals meet in a head-to-head orientation, engage in repeated and reciprocal tentacular contact ("flagellation"), move into a right-side-to-right-side position ("sidling"), and then lunge and bite at one another before they move apart. In this study, three types of interactions are analysed: 1) those with sidling (which in all cases was preceded by flagellation), 2) those without sidling but with flagellation, and 3) those with neither sidling nor flagellation.

The animals observed in this study were obtained at low tide from the rocks around the U.S. Highway 1 bridge abutment at Elkhorn Slough (Moss Landing, California). The animals were collected in June, 1979, and taken to the Long Coastal Marine Laboratory (Santa Cruz, California) for observation. In the laboratory, the animals were individually housed in small plastic cups approximately 6 cm in diameter and 7 cm deep. Each cup had its own supply of fresh, running sea water from a holding tank on the station property. The nudibranchs were fed fresh mussel (*Mytilus californianus*) every other day at

which time material remaining from the previous feeding was removed.

To observe their interactions, pairs of animals were placed in 1 to 2 cm of sea water in a 5 to 6 cm diameter watch glass. The ensuing interactions were recorded in writing or with a SONY Videorecorder (AV-3400 and AVC-3400) for detailed temporal analysis. For purposes of temporal analysis, the onset of an interaction was taken as the first physical contact between the animals and the end when the animals were separated by 1 cm or more.

The temporal structure of interactions with sidling is shown in Figure 1. The longest part of these interactions

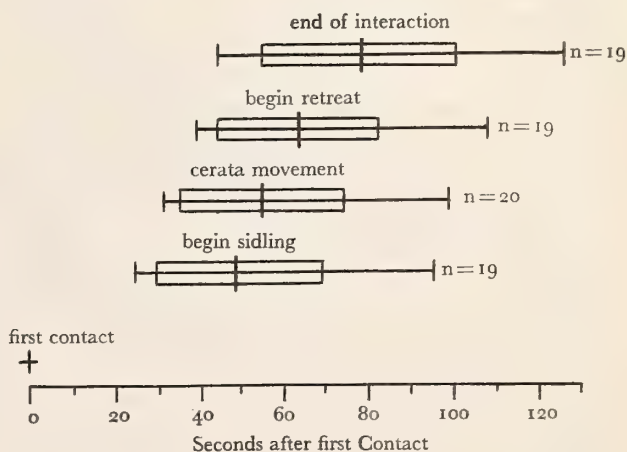


Figure 1

The temporal structure of head-to-head interactions with sidling. The mean time of occurrence, standard deviation (open bar), range, and sample size (n) are shown for each event

is from initial contact to the beginning of sidling, that is, when the animals engage in flagellation and slowly advance toward one another. The beginning of sidling is defined as the time when the animals' bodies first begin to overlap at the head, right-side-to-right-side. Forward movement stops when each animal has his head positioned approximately over the other animal's gonopore on the right side. At this point there is typically a brief pause just before both animals erect and elongate their cerata (Zack's "cerata movement"). One or both animals then begin biting and lunging at the other. One animal then turns away from the other and begins to move away, marking the beginning of retreat. The other animal typically follows briefly while lunging once or twice before the retreating animal moves out of range. Although the animals are poised in copulation-like posture during sidling, it seems clear, as Zack suggested, that these interactions are not copulatory since the time between initiation of sidling and cerata movement is on the average less than 10 sec. In opisthobranchs, copulatory durations are characteristically a matter of many minutes or hours rather than seconds (e.g. BEEMAN, 1970; KUPFERMANN & CAREW, 1974).

Interactions leading to sidling most frequently followed initial head-to-head contact (ZACK, 1975). Only 6% of the 18 interactions on the videotapes that did not begin head-

to-head lead to sidling. On the other hand, not all head-to-head interactions (46% of 39 on videotape) lead to sidling. These interactions were of two types, those with flagellation and those without, and these were temporally analysed for comparison with those head-to-head interactions that lead to sidling (Figure 2). Those interactions without sidling but with flagellation were not significantly different in overall duration from those with sidling and flagellation ($t=1.148$, 27 df, $p>0.10$). Also, the time from first contact until sidling began or one animal began retreat was not significantly different between the two types of interactions ($t=0.36$, 30 df, $p>0.36$) which indicates that when flagellation occurs it has some typical duration. Flagellation was usually terminated when one animal began lunging and biting at the other. The time from the beginning of retreat to the end of the interaction did not differ significantly between the two types of interactions with flagellation ($t=0.42$, 27 df, $p>0.33$).

Interactions without flagellation were significantly shorter than those with sidling and flagellation ($t=8.02$, 32 df, $p<0.0001$) and those with flagellation but no sidling ($t=4.62$, 23 df, $p<0.0001$). These encounters were characterized by one animal beginning to lunge at the other immediately after initial contact, hence the time from initial contact to the beginning of retreat was only a matter of a few seconds. The time from beginning of retreat to the end of the interaction was not significantly different from that for interactions with flagellation but without sidling ($t=0.203$, 23 df, $p>0.42$) or that for interactions with sidling and flagellation ($t=0.777$, 32 df, $p>0.22$).

These results are in general agreement with those of ZACK (1975) and show that those interactions involving sidling and, in particular, flagellation are substantially longer than those without these behavior patterns. It appears particularly likely that flagellation reflects efforts on the part of each participant to assess the aggressive motivation and possibly size of the other individual. Zack has shown large size to be an important variable determining success in these interactions. In addition, although these encounters have never been observed to end in copulation by Zack or this author, their form suggests that given the appropriate context and motivation on the part of the participants they may lead to copulation. Flagellation and sidling may also be means of assessing willingness to mate. Clearly, more detailed observations of these interactions are needed both in the field and under controlled laboratory conditions before reasonable proximate and ultimate explanations for their occurrence and form can be proposed.

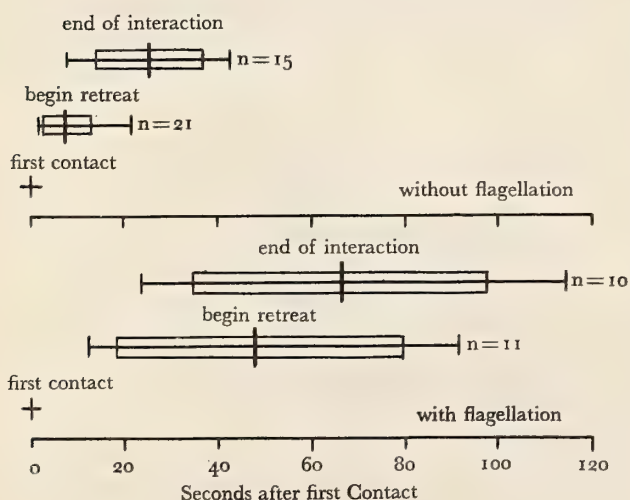


Figure 2

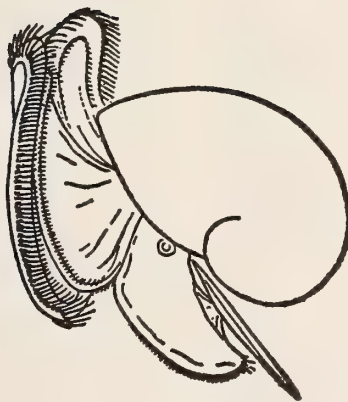
The temporal structure of head-to-head interactions without sidling. Above, interactions without flagellation; below, interactions with flagellation. The mean time of occurrence, standard deviation (open bar), range, and sample size (n) are shown for each event

ACKNOWLEDGMENTS

Thanks are given to John Schaeffer for his assistance in data reduction and analysis and to the Bache Fund of the National Academy of Sciences for financial support.

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Hermisenda: Agonistic Behavior or Mating Behavior?

BY

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MATING HAS NOT BEEN DESCRIBED in the colorful, intertidal eolid *Hermisenda crassicornis* (Eschscholtz, 1831) (Gastropoda: Nudibranchia), although its behavior (ZACK, 1975; LEDERHENDLER *et al.*, 1980), neurophysiology (FARLEY & ALKON, 1980; ALKON, 1980), and development (HARRIGAN & ALKON, 1978) have been the subject of recent studies. COSTELLO (1938) comments that the reciprocal copulation in hermaphroditic nudibranchs is a rather long process, taking hours or days for some species. The actual speed and character of the mating behavior which we describe here for *Hermisenda* are quite different, with the whole process of copulation requiring about one second. Some elements of this behavior have apparently been confused with aggression, giving this species an undeservedly vicious reputation.

Animals 25-60 mm long were placed together in a fingerbowl 90 mm in diameter and observed through a dissecting microscope for an hour, or less if copulation occurred. Courtship behavior in *Hermisenda* usually begins with one animal following and contacting the other animal with its tentacles until eventually the animals turn and meet anterior to anterior. Mutual contact between tentacles or between tentacles and cerata causes withdrawal, but contact of tentacles to the anterior edge of the opposite animal's foot results in an advance. This orientation requires several minutes, with many small advances and withdrawals. When the V-shaped groove at the anterior edge of each animal's foot comes into contact with the other, the orientation part of the behavior, characterized by rapid withdrawal and lunging, ceases. The alignment of the gonopores on the right side of each animal preparatory to copulation is more stereotyped than courtship and orientation. The animals move along the right side of one another, head to tail, with mutual contact to the edge of the foot until the gonopores are opposite each other. Up to this point, the orientation and alignment phases of the

behavior are similar to our observations on another nudibranch *Aeolidia papillosa* (to be published). The orientation time, from placing two *Hermisenda* together until foot contact, ranges from 10-30 minutes, while the alignment time, from foot contact until copulation, lasts about 1-3 minutes. With the gonopores in alignment, there is a brief surge as the animals draw together, evert penes, emit sperm, and separate, all in an interval of 1-2 seconds. As the penis is everted, its end expands into a translucent bulb which usually, but not always, strikes the vaginal opening of the opposite animal. Penis eversion, apparently by muscular contraction, and sperm ejaculation occur too quickly for direct visual evaluation. The active sperm, which pass through a short vas deferens (1-5 mm), are emitted in a transparent mucus which slows their diffusion into the surrounding seawater. After separation, encounters between the animals are brief, with mutual avoidance.

The remarkable speed of copulation and the abruptness of the associated body movements lend a deceptively agonistic appearance to mating in *Hermisenda*. Many of the intraspecific interactions described by ZACK (1975) appear to be mating behavior despite his statement that he never observed copulation; his apt terms "flagellation" and "sidling" describe, respectively, orientation and alignment for copulation in this species. Experience with *Aeolidia papillosa* greatly aided our recognition of mating in *Hermisenda*, but it was only after we removed the anterior cerata covering the genital opening that we were able to confirm that copulation did in fact occur. In seven hours of observation during which 10 matings occurred in 4 pairs of animals, we did not see damage inflicted by biting as described by ZACK (1975), but the delicate maneuvers occurring in the initial orientation and the readiness of the animal to withdraw from contact may be behavioral responses which have evolved to reduce the probability of being eaten prior to copulation. Such inadvertent behavior (for the consumed animal) has been reported in connection with mating in *Navanax* (PAINE, 1965).

¹ Address for correspondence

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Editor's Note:

On October 10, 1980 we received the manuscript by Dr. R. L. Rutowski. In the review process a few minor questions were raised. These were passed on to Dr. Rutowski for his consideration on 26 December 1980. Unfortunately, Dr. Rutowski was unable to respond until May 20, 1981. The manuscript was re-submitted to the original referees and their recommendation to accept the manuscript for publication arrived shortly afterward. On June 20, 1981, the manuscript by the Drs. Longley arrived. The referees recommended publication.

In preparing the manuscripts for publication, your editor became aware that, although both articles dealt with similar observations of behavior of the same species, conclusions reached seemed to differ. Had Dr. Rutowski been

able to respond within the usual time, his paper would have been published and it would have been available to the Drs. Longley. It seemed in the interest of all concerned — authors and prospective readers of the articles — to give both authors a chance to review each other's work and, if desired, discuss their differences by correspondence and submit, for simultaneous publications with the original papers such comments as they deemed desirable. This procedure, it was thought, would keep all the facets of the situation together and would at the same time avoid that future workers might have to hunt through several issues of the same journal or through several different journals to get the whole story.

We are pleased to present herewith the comments from both parties.

Your Editor.

From Dr. Rutowski, the following comments were received on September 8, 1981:

"To: R. Stohler

"From: R. L. Rutowski

"Re: Comments on papers by Longley and Longley and by Rutowski

"I have read the Longley's paper on mating in *Hermisenda* with great interest and congratulate them for providing evidence bearing on the function of the enigmatic interactions described by Zack and myself. I see no major conflict between their results and mine which deal strictly

with the temporal structure of the various types of interactions observed in *Hermisenda* and not with their function. My assumption, that the interactions with sidling that I observed were aggressive and not copulatory, was based on the best available information at the time of submission of my manuscript. Obviously, this assumption must now be re-evaluated. It should be emphasized, however, that the Longleys' article deals with only one type of interaction. Zack's work makes it clear that many of the other possible outcomes and forms these interactions may take are markedly aggressive.

"There are several small discrepancies between the results reported in the two articles that bear brief discussion. First, the Longleys' note suggests that courtship leading to copulation usually begins with one animal following and contacting another, that is, initial head-to-tail contact. However, Zack's results and those I have reported strongly suggest that sidling, an apparent preliminary to copulation, is most likely to occur after initial head-to-head contact. Second, the Longleys' information on the duration of some phases of the courtship is at variance with my data on the temporal structure of interactions with sidling. Finally, it is not clear from their statement on biting and lunging after mating if these behavior patterns did not occur or did occur but did not result in damage. Two factors make the causes of these discrepancies difficult to evaluate. One is the qualitative nature of the Longleys' observations and the other is the lack of detail with respect to the methods they used to make their observations.

"In sum, aside from these minor problems in interpretation and comparison, nothing in my report disallows the Longleys' proposal that interactions with sidling are copulatory. While awaiting a more quantitative account that includes more detailed descriptions of their procedures, I gladly, if somewhat cautiously, support their hypothesis."

From the Drs. Longley, the following comments were received on September 14, 1981:

"To: Editor, The Veliger

"Re: Mating in *Hermisenda*

"The primary purpose of our paper on mating in *Hermisenda* was to suggest that the principal conspecific interactions in this species involve mating rather than agonistic behavior. We hoped with this qualitative description of the mating behavior to bring about a re-evaluation of previous work on agonistic behavior in this species. We are pleased that Dr. Rutowski is facilitating this process, but regret the untimely collision of our articles. In the following we will attempt to answer some of the questions raised by Dr. Rutowski's comments on our paper.

"We divided mating into orientation, alignment, and copulation, and estimated a range of duration for these phases while observing 10 matings. We have not seen Dr. Rutowski's figures which give his quantitative results, but our orientation phase, operationally defined as beginning when the animals are placed together, and our alignment

phase, prior to copulation, apparently do not coincide with his behavioral segments based on the distance separating the animals, where the animals were assumed to be engaging in agonistic behavior.

"Our statement on biting and damage inflicted by biting accurately reflects our observations. *Hermisenda* is quite capable of inflicting damage with the sharp serrations in its jaws, but although we looked for such biting for seven hours while viewing the animals through the dissecting microscope, we were unable to observe any instance where the buccal mass was extended and a part of the other animal bitten. We cannot entirely exclude such a possibility, though, with unrecorded direct visual observation. Neither can we exclude the possibility that dominance is communicated by some means other than biting, since in one instance we did see withdrawal of one member of a trio which was attempting simultaneous alignment of the gonopores.

"When the behavior is viewed as a whole, the initial part of the orientation did usually begin with one animal following the other, but head-to-head contact is, as we have pointed out, a necessary part of the mating process. Even when the initial contact is head-to-head, which may be more likely in a small container than in a natural setting, it will not necessarily lead immediately to alignment and copulation since it requires that both members of the pair be prepared to mate. Such encounters where only one member of a pair is ready to mate may be mistakenly regarded as agonistic. Where the behavior may be initiated by one animal, but where both animals must be motivated to interact in the appropriate stereotypic manner before mating can take place, it does not follow that segments of the behavior which do not lead to copulation are examples of agonistic behavior.

"Zack remarks that he would class the vast majority of the encounters he observed between two *Hermisenda* as non-agonistic and that he was unable to observe agonistic behavior in the field. We think that intraspecific agonistic behavior does not occur in this species in the field, except possibly under overcrowded conditions where two or more animals are contesting for a small food item or for mating preference, and this activity remains to be demonstrated as an important part of the behavioral repertoire of *Hermisenda*."

"Roger D. Longley and Alison J. Longley
Friday Harbor Laboratories
Friday Harbor, WA 98250"

Morphological Characterization of the *Littorina scutulata* Species Complex

BY

TALBOT MURRAY

Fisheries Research Division, P. O. Box 297, Wellington, New Zealand

(2 Text figures)

INTRODUCTION

GOULD (1849) DESCRIBED THREE SPECIES OF *Littorina* (*L. lepida*, *L. plena* and *L. scutulata*) from the north-eastern Pacific coast that have subsequently been considered as morphological variants of *L. scutulata*. On the basis of reproductive characteristics, however, MURRAY (1979) demonstrated that this taxon was a mixture of two species but was unable to identify morphological differences between the two species. The confounding of the two species has remained a problem, due to the variance and degree of overlap in univariate morphometric characteristics. In this paper I have employed the multivariate statistical techniques of discriminant analysis to identify morphological differences between the reproductive types of MURRAY (*op. cit.*) and principal component analysis to describe size and shape variation between the two species. It was also possible using discriminant analysis to classify existing type material to one of the two species and to identify synonymies in GOULD's (1849) material.

This study would not have been possible without the loan of type material by Dr. J. Rosewater, U.S. National Museum of Natural History, Washington, D.C. and Dr. K. J. Boss, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts for which I am grateful.

METHODS

Statistical analyses were based on whorl number, shell length, whorl height, width perpendicular to the columellar axis, maximal width, shell depth and apical angle of preserved females of known spawning history from MURRAY's (1979) study. Linear measurements were taken with a pair of vernier calipers to the nearest 0.01 mm (see

Figure 1). Apical angle (in radians) was derived as the arc tangent of the shell length: maximal width ratio. All measurements were made with the aperture oriented upwards. The discriminant and principal component analyses were conducted using the Biomedical Computer Programs—P series library version BMDP-77 developed by the Health Sciences Computing Facility, UCLA, Los Angeles, California. The discriminant analysis (BMDP-7M, program revised November 1979) employed a stepwise variable entry procedure followed by stepwise variable removal to maximise the generation of alternative models for highlighting morphological differences (see DRAPER & SMITH, 1966). The classification of individuals to species was based on a jackknife estimation procedure in order to minimise bias. Principal components were extracted from the covariance matrix of log transformed measurements of shell length, whorl height, width perpendicular to the columellar axis, maximal width and shell depth after the suggestion of JOLICOEUR (1963) using BMDP-4M (program revised November 1979). Whorl number could not be included because it is measured in units that give it a minimal contribution to the principal components (JOLICOEUR, *op. cit.*).

Morphological Differences Associated with Reproductive Types within the *Littorina scutulata* Complex

The earlier study of MURRAY (1979) established that two species were being confounded as *Littorina scutulata*. However, without knowledge of the age of individuals the differences in the means of the morphometrics could not be ascribed to species differences. In addition, the overlap in the distributions of each character meant that uni-

variate traits could not be used to tell the species apart reliably.

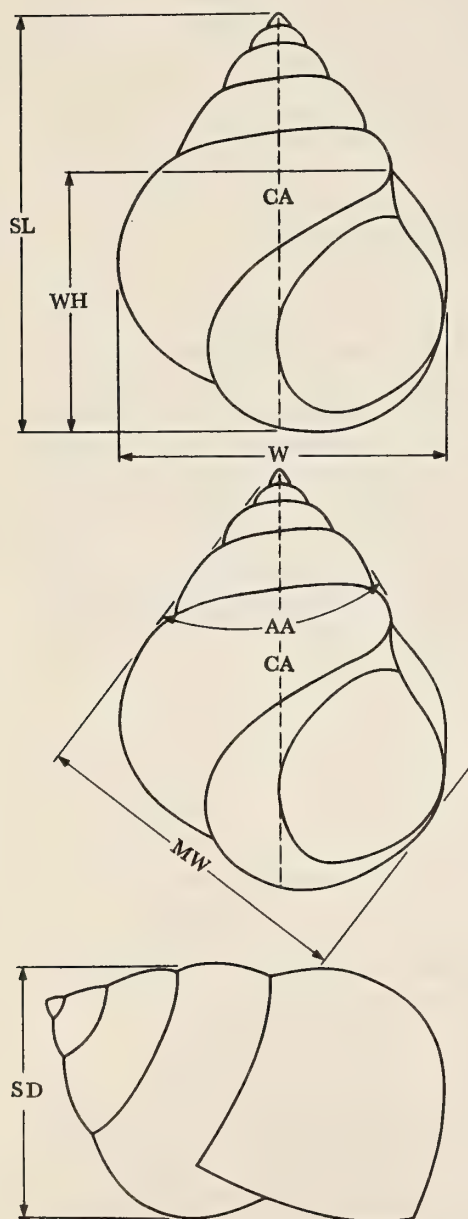


Figure 1

Morphological measurements made on each shell.

AA - apical angle CA - columellar axis
MW - maximal width SD - shell depth SL - shell length
W - width WH - whorl height

Discriminant analysis is ideally suited to the resolution of such problems. It is an extremely robust procedure that allows one to combine morphometrics (*e.g.*, lengths, weights, angles, etc.) with morphological traits (*e.g.*, number of whorls, presence or absence of a trait, etc.) to construct divisive criteria amongst groups known to be distinct based on some independent criterion. The divisive criteria are linear functions of morphological characters that yield the widest separation of groups. In the present application we know the two species differ in their reproductive characteristics and hypothesize the existence of an unknown set of concomitant morphological differences. We do not know *a priori* what this set will be, hence we employ a stepwise variable entry procedure that will produce a maximum number of alternative discriminant models. We subsequently choose the set of variables that yields discriminant functions with the highest proportion of correct classifications of reproductive types and of type material. If the probability of correctly classifying individuals is sufficiently better than by chance, we accept our hypothesis that there exist morphological differences between the reproductive types. We can then employ these functions to identify individuals of unknown reproductive history.

In this study the best discriminant model for separating the two species is the following pair of four variable functions: $Z_1 = 15.71X_1 - 12.21X_2 + 20.58X_3 + 4.75X_4 - 51.48$; $Z_2 = 13.34X_1 - 20.39X_2 + 33.06X_3 + 12.11X_4 - 70.57$ where: X_1 = whorl number, X_2 = shell length, X_3 = whorl height, and X_4 = shell depth. The classificatory power of these functions is indicated in Table 1. With these functions 95.6% of the specimens known to be *Littorina scutulata* were correctly classified and 96.0% of the specimens known to be different from *L. scutulata* were also correctly classified. Type material of *L. scutulata*, with the exception of 3 of 5 idiotypes from San Francisco (MCZ 169360), was also correctly classified. It seems probable that this sample and that of USNM 796179 are mixtures of the two species, since the probability of misclassification is small (4%) and the collecting locality is an area where both species commonly co-occur (MURRAY, 1979).

Type material of *Littorina plena* and *L. lepida* was consistently classified as different from *L. scutulata*. Since the type specimens of *L. plena* and *L. lepida* cannot be distinguished from each other, they should be regarded as conspecific. As first reviser I propose the reinstatement of *Littorina plena* (to be described later in this paper) for the other member of the *L. scutulata* complex. *Littorina lepida* should be regarded as a synonym of *L. plena*. I regard *L. plena* as a preferable name, since

Table 1

Classification of material examined based on discriminant analysis of *Littorina scutulata* reproductive types I and II of MURRAY (1979).

Group	% correctly classified	Number of cases classified as		Comments
		<i>Littorina scutulata</i>	Not <i>Littorina scutulata</i>	
<i>Littorina scutulata</i>	95.6	43	2	Murray's (1979) Type II ♀ ♀
Not <i>Littorina scutulata</i>	96.0	2	48	Murray's (1970) Type I ♀ ♀
MCZ 169222	100.0	0	4	<i>Littorina lepida</i> syntypes, Puget Sound
MCZ 169289	100.0	0	2	<i>Littorina plena</i> idiotypes, San Francisco
MCZ 169360	mixture	2 ¹	3	<i>Littorina scutulata</i> idiotypes, San Francisco
USNM 5635	100.0	0	1	<i>Littorina plena</i> type, San Francisco
USNM 5637	100.0	1	0	<i>Littorina scutulata</i> figured type, Puget Sound
USNM 5640	100.0	1	0	<i>Littorina scutulata</i> holotype, Puget Sound
USNM 612308	100.0	1	0	<i>Littorina scutulata</i> paratype, Puget Sound
USNM 677095	100.0	0	1	<i>Littorina lepida</i> paratype, Puget Sound
USNM 677096	100.0	0	2	<i>Littorina plena</i> paratype, San Francisco
USNM 796179	mixture	4 ²	6	<i>Littorina scutulata</i> from San Francisco

¹shell lengths = 10.33, 8.18 mm

²shell lengths = 5.95, 8.55, 8.60, 8.95 mm

the description of GOULD (1849: 84) more closely describes the specimens I have observed than does his description of *L. lepida* (GOULD, 1849: 83) thereby overriding page precedence of the Law of Priority (article 24 of the ICZN).

The discriminant functions Z_1 and Z_2 have a wider utility outside the scope of this paper. Since the two species are easily confused, these functions can be used in future studies to improve the accuracy of identification using four easily measured shell characters. The following example demonstrates how the functions Z_1 and Z_2 are used. We collect a shell and record its number of whorls (X_1) as 5.0, shell length (X_2) as 8.10 mm, whorl height (X_3) as 4.59 mm, and shell depth (X_4) as 4.69 mm. We then calculate values for Z_1 and Z_2 given these data. We classify our specimen according to the following inequalities: if $Z_1 < Z_2$ the specimen is *Littorina scutulata*, if $Z_1 > Z_2$ the specimen is *L. plena*. In our example we calculate values of $Z_1 = 44.91$ and $Z_2 = 39.51$, therefore, since $Z_1 > Z_2$ we predict (with greater than 95% certainty) that the specimen is *L. plena*. This technique is extremely powerful and has been used by MURRAY (1980) to demonstrate morphological differences within a species due to tidal height and parasitism. The reader should bear in mind that these functions do not take into account morphological variation that might exist between sexes, tidal level, or differences that result from other environmental sources. This cautionary note does not denigrate the utility

of these functions but they should be used with caution. They are included because we expect that differences between species are greater than differences within a species.

Morphological Variation in Size and Shape in *Littorina scutulata* and *Littorina plena*

Thus far we have assumed different shell morphologies between species and used these differences without characterizing them. We can now proceed to develop multivariate measures of size and shape for *Littorina scutulata* and *L. plena*, using principal component analysis. The advantage of this technique is that it allows one to develop the best single descriptions of mutually independent trends in size and shape variability. Best is used in the sense that each trend maximally explains the observed variation in morphology with respect to that trend. For example, each description of size variation (= first principal component) maximally describes the variability that can be attributed to variation in shell morphology associated with differences in size among specimens. The remaining information about morphology is explained by variation in shape that is independent of size and derived from the residual variance of the first principal component. This process is continued until the information gained at each extraction tails off.

Variation in size and shape together explain more than 98% of the total variation in shell morphology in *Littorina scutulata* and in *L. plena*, so additional principal components were not extracted. Most of the variation in morphology is associated with size related variation, as can be seen from Table 2 (97.3% for *L. scutulata* and 97.5% for *L. plena*). Variation in morphology attributable to shape is small (1.3% for *L. scutulata* and 1.9% for *L. plena*). Although shape is a small component of morphology, it is shape variation that exhibits the greatest difference between species and probably accounts for our ability to separate *L. scutulata* and *L. plena* morphologically. This becomes readily apparent when we calculate the angle between each trend in variation. It should be borne in mind that each principal component is a vector (whose elements are the coefficients in Table 2) extending through

Graphically, we can view each trend as a morphological continuum with a greater separation of the species along the shape continuum than along the size continuum. This separation of species along the shape continuum is evident in Figure 2. The ellipses have been drawn in to delimit the groups and do not represent confidence ellipses. This figure does serve to dramatize the different morphologies for *Littorina scutulata* and *L. plena*. We can now describe the characteristics of each and highlight the differences between species.

Littorina scutulata Gould, 1849

holotype: USNM 5640, collected Puget Sound, shell length = 12.16 mm

paratype: USNM 612308, collected Puget Sound, shell length = 8.79 mm

Table 2

Coefficients of size and shape functions for *Littorina scutulata* and *Littorina plena*.

	<i>Littorina scutulata</i>		<i>Littorina plena</i>	
	size variation (1st P.C.)	shape variation (2nd P.C.)	size variation (1st P.C.)	shape variation (2nd P.C.)
Log shell length	0.4907	0.2659	0.5012	0.2152
Log whorl height	0.4083	-0.2926	0.3740	-0.4460
Log width	0.4399	-0.4361	0.4216	-0.3823
Log maximal width	0.4267	-0.3640	0.4187	-0.3317
Log shell depth	0.4657	0.7202	0.5062	0.7080
Variance $\times 10^4$	229.86	3.11	414.11	7.98
% total variance	97.30	1.32	97.53	1.88

a cluster of points that represents the shell geometry of each species. Since it is a vector, we can calculate the angle between principal components as a measure of the difference between species. If we take $U_1 = u_{11}, u_{12}, u_{13}, u_{14}, u_{15}$ as the vector of coefficients associated with size variation in *L. scutulata* and $V_1 = v_{11}, v_{12}, v_{13}, v_{14}, v_{15}$ as the vector of coefficients associated with size variation in *L. plena* then the angle between U_1 and V_1 is given by: $\cos \theta = u_{11} v_{11} + u_{12} v_{12} + \dots + u_{15} v_{15}$ (JOLICOEUR, 1963). The more similar the trends the smaller the angle θ . Using the coefficients in Table 2 we calculate an angle of 3.1° between the trends in size variation in *L. scutulata* and *L. plena*. Shape variation between the species is more widely divergent and is separated by an angle of 9.9° . Shape differs more than size between species.

Littorina scutulata are small obconic brown snails of the mid-littoral zone. Adult snails typically have 5 whorls and can be expected to range in size from 11.3 mm to 11.9 mm (mean shell length = 11.61 mm). Infrequently (15.9% of the snails observed) the base of the body whorl will be marked by an indistinct ivory colored band which may also be visible as a stripe inside the aperture. The apical angle is typically 30.4° . Morphological characters are summarized in Table 3. The reproductive features of this species definitively identify it (MURRAY, 1979). Males possess a penis with a conspicuous sperm groove running dorsally to a sub-terminal bulge. Female *L. scutulata* produce characteristic pelagic egg capsules shaped like inverted saucers 0.7 to 1.0 mm in diameter and containing 1 to 14 eggs $105 \mu\text{m}$ in diameter.

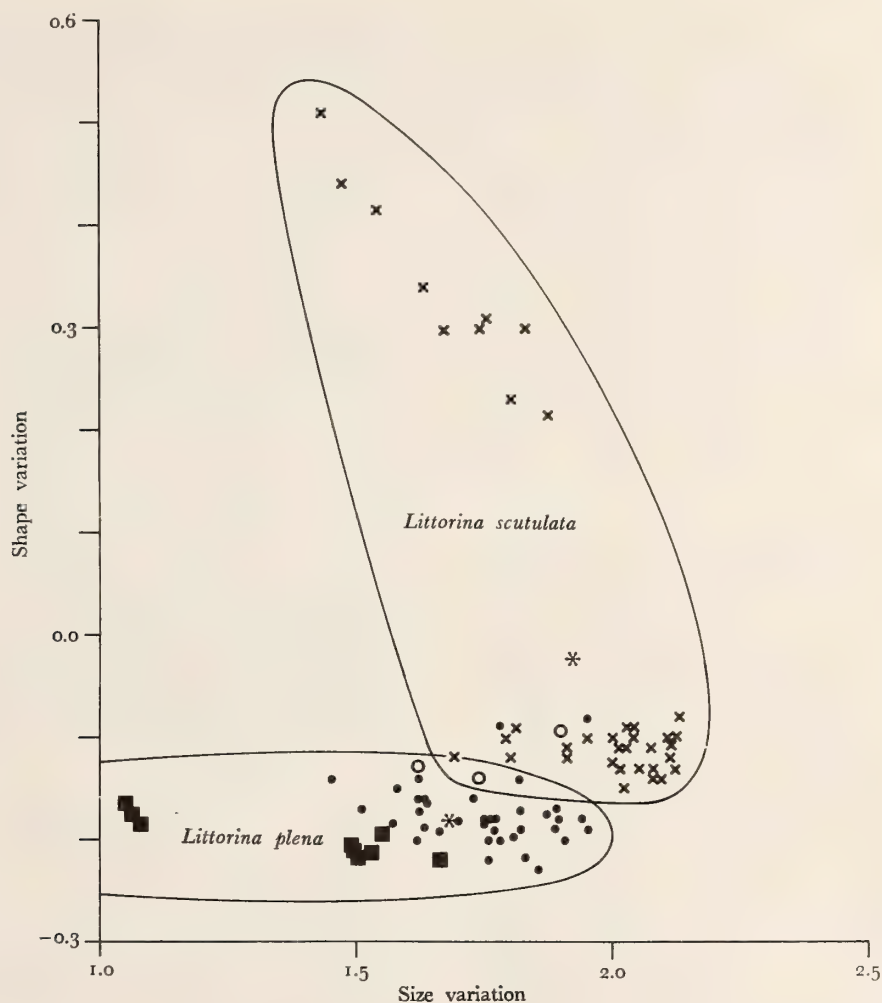


Figure 2

Scatterplot of size versus shape variation in *Littorina scutulata* and *Littorina plena*

Asterisks (*) represent the mean of each group; × represents *Littorina scutulata* from Dillon Beach, California; open circles (○) *L. scutulata* from Rockport, California; closed circles (●) *L. plena* from Newport, Oregon; closed squares (■) *L. plena* from Dillon Beach, California. Values of size and shape variation were calculated from the coefficients in Table 2

Littorina plena Gould, 1849

(synonym: *Littorina lepidus* Gould, 1849)

holotype: USNM 5635, collected San Francisco, shell length = 8.52 mm

paratypes: USNM 677096, collected San Francisco, shell lengths = 6.22, 8.20 mm

The morphological characteristics of *Littorina plena* are summarized in Table 3. Although this species is morphologically similar to *L. scutulata*, adults are generally smaller (8.4 mm < shell length < 8.9 mm as opposed to 11.3 mm < shell length < 11.9 mm). *Littorina plena* as noted by GOULD (1849) also tend to be more ovate, having

Table 3

Summary of the morphological characteristics of
Littorina scutulata and *Littorina plena*.

	<i>Littorina scutulata</i>		<i>Littorina plena</i>	
	mean (\pm 1 S.E.)		mean (\pm 1 S.E.)	
Whorl number	5.09	(0.08)	5.40	(0.10)
Shell length (mm)	11.61	(0.28)	8.60	(0.25)
Whorl height (mm)	7.00	(0.14)	4.87	(0.11)
Width (mm)	7.81	(0.17)	5.44	(0.13)
Maximal width (mm)	6.84	(0.52)	6.35	(0.16)
Shell depth (mm)	6.37	(0.15)	4.53	(0.14)
Apical angle (radians)	0.53	(0.04)	0.64	(0.004)
Size (1st P.C.)	1.92	(0.03)	1.68	(0.03)
Shape (2nd P.C.)	-0.02	(0.03)	-0.18	(0.004)
Frequency of band on the base of the body whorl	15.9%		84.3%	
n	45		50	

an apical angle of 36.7° as opposed to 30.4° in *L. scutulata*. The ivory band present but indistinct in 15.9% of *L. scutulata* is more prominent in *L. plena* and occurs on 84.3% of the shells studied. The coloration of *L. plena* shells is also more variable than *L. scutulata* and ranges from dark brown to brown tessellated with grey. As in *L. scutulata*, the reproductive features described by MURRAY (1979) definitively characterize this species. Male *L. plena* have a penis in which the sperm groove runs laterally to the tip instead of dorsally as in *L. scutulata*. The penis of *L. plena* also bears a prominent papilla on the dorso-lateral surface proximal to the curvature of the penis. This papilla is absent in *L. scutulata*. Female *L. plena* also differ from *L. scutulata* in the characteristics of their spawn. Female *L. plena* produce pelagic egg capsules that resemble automobile wheels slightly greater than 1 mm in diameter and contain from 4 to 41 eggs $95.7 \mu\text{m}$ in diameter.

CONCLUSIONS

Discriminant analysis verified the hypothesis that in addition to the reproductive differences in *Littorina scutulata* species complex reported by MURRAY (1979) there exist associated morphological differences. Using principal components it was possible to demonstrate that most of

the difference in morphology between species could be attributed to a separation along a multivariate shape continuum. However, the primary purpose of this study is to provide a way of minimizing the confounding of *Littorina scutulata* and *L. plena* in future studies. The ease with which these species can be distinguished is ultimately dependent upon the level of accuracy a researcher is content with. If a researcher is content with an approximate 16% chance of error, then *L. plena* can be distinguished by the presence of an ivory band on the base of the body whorl and its generally smaller size. This error rate, however, can be reduced to approximately 4% by counting the number of body whorls, measuring shell length, whorl height and shell depth and employing the discriminant functions derived in the text. If a 4% error rate is unacceptable, the two species can be distinguished with absolute certainty only by recourse to the reproductive characteristics described by MURRAY (1979). In addition to the low error rate, the discriminant functions have the additional advantages that they do not require snails in breeding condition; they work equally well on empty shells as on live material; the necessary measurements are easily made and usually of considerable interest in a study; and the calculations necessary to determine species identity are readily done on a hand calculator.

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Littorina scutulata and *Littorina plena*:
Sibling Species Status of Two Prosobranch Gastropod Species
Confirmed by Electrophoresis

BY

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(4 Text figures)

INTRODUCTION

THE INTRODUCTION OF BIOCHEMICAL TECHNIQUES to modern taxonomic procedures has confirmed the presence of numerous sibling species whose identities were originally suspected on the basis of slight differences in morphological, cytological, or ecological characters. The most comprehensive studies using such techniques concern species complexes of *Drosophila* (HUBBY & THROCKMORTON, 1968; AYALA *et al.*, 1970; AYALA & POWELL, 1972; YANG *et al.*, 1972; COYNE, 1976). However, biochemical methods have also provided evidence of sibling species for a wide array of marine organisms, including polychaetes (GRASSLE & GRASSLE, 1976; NICKLAS & HOFFMAN, 1979), seastars (SCHOPF & MURPHY, 1973), sea cucumbers (MANWELL & BAKER, 1963), barnacles (HEDGEcock, 1979; DANDO & SOUTHWARD, 1980), fiddler crabs (SALMON *et al.*, 1979), limpets (MURPHY, 1978), and sea anemones (BUCKLIN & HEDGEcock, 1981). In each instance, biochemical data have indicated genetic isolation and have provided diagnostic characters for distinguishing between closely-related sibling species.

Snails currently classified as *Littorina scutulata* Gould, 1849, are upper littoral gastropods of the west coast of North America. They are abundant residents on rocks and pilings in sheltered bays as well as on rocky shores of the exposed open coast. MURRAY (1979) has shown that a dichotomy exists in the reproductive biology of *L. scutulata*. A dimorphism of genitalia occurs among males, and individual females produce one of two morphologically distinct types of planktonic egg capsules, differing in size, in shape, in numbers of eggs per capsule, and in the location of the hatching pore through which swimming veligers

emerge. Developmental rates within the two types of egg capsules also appear to differ, further suggesting that the taxon *L. scutulata* is actually a complex of two morphologically similar species.

The purpose of this study is to assess the degree of genetic and reproductive separation between the two morphological forms of *Littorina scutulata*. The techniques of gel electrophoresis are employed to confirm their taxonomic status as separate species. We suggest that the name *Littorina plena* Gould, 1849, be revived for the second sibling species.

MATERIALS AND METHODS

Populations Studied

Adult snails belonging to the *Littorina scutulata* species complex were collected at random from rocky shores at 15 localities (Figure 1). These samples were taken at irregular intervals from the summer of 1979 through the summer of 1980. Samples from the following five sites in California were selected for detailed study by horizontal starch gel electrophoresis: Newport Beach, Orange County (NB); Shell Beach, San Luis Obispo County (SLO); Bodega Bay (BB) and Sea Ranch (SR), Sonoma County; and Point Arena, Mendocino County (PA). Other observations were made on snails from additional sites in California: Bird Rock, San Diego County (SD); Laguna Beach, Orange County (LB); Goleta, Santa Barbara County (SB); Pacific Grove, Monterey County (MON); Berkeley Marina inside San Francisco Bay (SF); Dillon Beach, Marin County (DB); and Trinidad, Humboldt County (HUM). Collections were also made at Cape

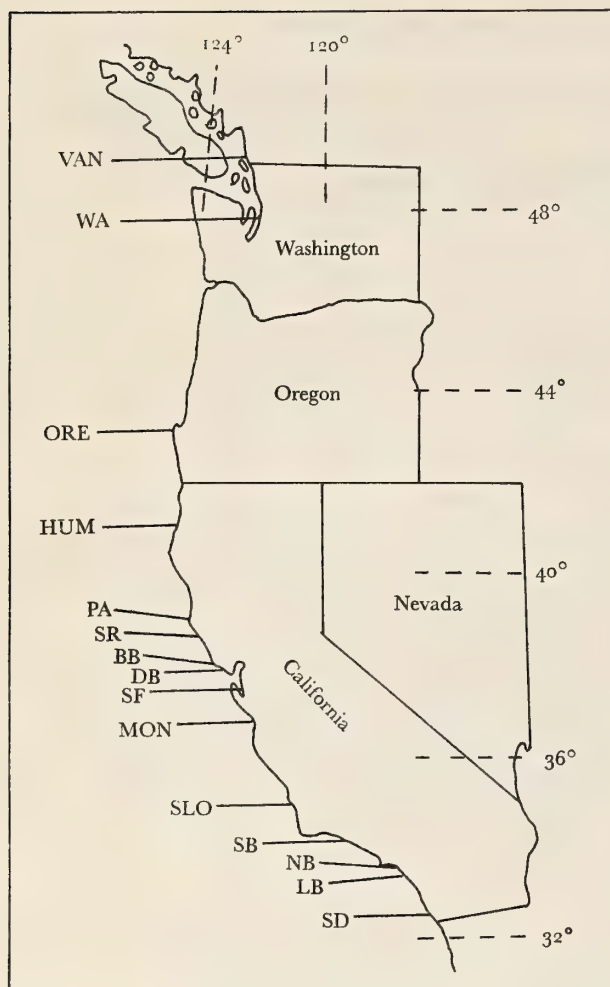


Figure 1

Map of California, Oregon, and Washington showing the approximate locations of sampling sites

Arago, Oregon (ORE), at several sites within Puget Sound, Washington (WA), and at Vancouver, Canada (VAN).

Snails were either transported directly or sent live by first class mail to the University of California Bodega Marine Laboratory. Individuals were separated by sex and by reproductive type (species) according to the characters described by MURRAY (1979). Male snails were identified by penis morphology and female snails by the type of egg capsules produced once isolated in individual containers. Only identifiable snails (reproductively active females and males with shell lengths greater than 4 mm) were used in the electrophoretic study.

Sample Preparation and Assay Technique

Snails selected for electrophoresis were maintained in running seawater without food for at least 48 hours after collection, and then were kept frozen at -80°C if not used immediately. Animals were removed whole from their shells, and the tissues were homogenized with an approximately equal volume of 0.5 M tris-HCl buffer (pH 7.1) while submerged in an ice-water bath. A small amount of the homogenate was absorbed with Whatman No. 1 filter paper wicks for insertion into starch gels.

Electrophoretic procedures were carried out essentially as described by AYALA *et al.* (1972). Samples of 23 snails were run in each gel along with two control samples. Controls consisted of individuals whose isozyme mobilities were previously determined. Each gel included snails of both reproductive morphologies.

The following five buffer systems were used to separate the ten enzymes assayed in all populations: (A) Discontinuous, tris-citrate electrode buffer, pH 8.65, borate (NaOH) gel buffer, pH 8.1 (AYALA *et al.*, 1973); (B) Continuous, tris-borate-EDTA electrode and gel buffer, pH 9.1 (AYALA *et al.*, 1973); (C) Continuous, tris-citrate-EDTA electrode buffer, pH 7.0, with a 15-fold dilution of the electrode buffer for the gel buffer (AYALA *et al.*, 1973); (D) Continuous, citric acid-phosphate electrode and gel buffer, pH 7.0 (SHAW & PRASAD, 1970); (E) Discontinuous, LiOH-boric acid electrode buffer, pH 8.1, tris-boric acid-citric acid LiOH gel buffer, pH 8.2 (SELANDER *et al.*, 1971). The buffer system used for each enzyme assay is specified in Table 1.

Enzyme-staining assays were conducted as described by AYALA *et al.* (1972, 1973, 1974) and by TRACEY *et al.*

Table 1

Enzymes assayed in *Littorina scutulata* and *Littorina plena* populations.

Enzyme	Abbreviation	Buffer system
Acid phosphatase	ACPH-2	A
Esterase	EST	E
Glutamate oxaloacetate transaminase	GOT	D
Leucine amino peptidase	LAP-1	A
Lactate dehydrogenase	LDH	B
Mannose-6-phosphate isomerase	MPI	D
6-Phosphogluconate dehydrogenase	6-PGDH	C
Phosphoglucose isomerase	PGI	E
Phosphoglucomutase	PGM	C
Sorbitol dehydrogenase	SDH	D

Table 2

Allelic frequencies of the ten loci examined for populations of *Littorina scutulata* and *Littorina plena*.
The value *n* equals the number of alleles sampled in each population.

Locus	Allele	<i>Littorina scutulata</i> populations					<i>Littorina plena</i> populations				
		PA	SR	BB	SLO	NB	PA	SR	BB	SLO	NB
<i>AcpH-2</i>	<i>n</i>	18	18	20	20	20	22	20	20	20	20
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>Est</i>	<i>n</i>	18	20	64	20	20	18	18	32	20	26
	98	0.39	0.65	0.44	0.40	0.63	—	0.11	—	0.10	0.08
	100	0.61	0.35	0.56	0.60	0.31	0.05	0.45	0.56	0.40	0.42
	102	—	—	—	—	0.06	0.77	0.33	0.44	0.50	0.50
	103	—	—	—	—	—	0.18	0.11	—	—	—
<i>Got</i>	<i>n</i>	18	32	20	20	34	22	28	20	20	32
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>Lap-1</i>	<i>n</i>	18	20	40	20	20	22	20	42	20	20
	100	0.78	0.50	0.55	0.70	0.55	0.77	0.60	0.38	0.65	0.45
	101	0.22	0.50	0.45	0.30	0.45	0.23	0.40	0.62	0.35	0.55
<i>Ldh</i>	<i>n</i>	18	36	46	20	32	22	20	24	20	16
	98	0.11	—	—	—	—	—	—	—	—	—
	100	0.89	0.97	1.00	1.00	1.00	0.18	0.20	—	0.45	0.31
	103	—	0.03	—	—	—	0.82	0.80	1.00	0.55	0.69
<i>Mpi</i>	<i>n</i>	18	20	10	20	40	22	20	10	20	40
	98	—	—	—	0.20	—	—	—	—	0.10	0.25
	100	1.00	1.00	1.00	0.75	1.00	1.00	1.00	1.00	0.55	0.75
	102	—	—	—	0.05	—	—	—	—	0.35	—
<i>6-pgdh</i>	<i>n</i>	18	32	64	20	34	22	18	66	20	24
	94	—	0.03	—	—	0.24	—	—	—	—	—
	96	—	—	—	—	—	—	—	0.03	—	—
	100	1.00	0.94	0.97	1.00	0.76	0.91	0.78	0.73	0.70	0.79
	103	—	0.03	0.03	—	—	0.09	0.22	0.24	0.30	0.21
<i>Pgi</i>	<i>n</i>	18	36	64	20	34	22	28	66	20	32
	90	0.05	—	0.01	—	0.06	—	—	—	—	—
	93	—	0.14	—	0.05	0.03	—	—	—	—	—
	96	0.17	0.11	0.19	0.25	0.15	—	—	—	—	—
	100	0.78	0.47	0.50	0.45	0.38	0.05	—	—	0.05	—
	103	—	0.28	0.19	0.25	0.32	0.63	0.68	0.74	0.75	0.72
	106	—	—	0.11	—	0.06	—	—	—	—	—
	107	—	—	—	—	—	0.27	0.32	0.24	0.20	0.25
	110	—	—	—	—	—	0.05	—	0.02	—	0.03
<i>Pgm</i>	<i>n</i>	18	34	64	20	34	22	28	66	20	32
	97	—	0.15	—	0.05	0.03	—	—	—	—	—
	100	0.39	0.53	1.00	0.65	0.73	—	0.10	—	—	—
	102	0.57	0.26	—	0.30	0.21	0.64	0.75	0.70	0.75	0.78
	105	0.04	—	—	—	0.03	0.23	0.04	0.26	0.20	0.09
	107	—	0.06	—	—	—	—	0.04	—	0.05	0.13
	110	—	—	—	—	—	0.13	0.07	0.04	—	—
<i>Sdh</i>	<i>n</i>	18	34	14	20	20	22	22	24	20	20
	94	—	0.03	—	—	—	—	—	—	—	—
	100	1.00	0.97	1.00	0.90	0.85	0.14	0.18	0.29	0.30	0.40
	102	—	—	—	0.10	—	—	—	—	—	—
	107	—	—	—	—	0.15	0.86	0.82	0.71	0.70	0.60

(1975) with the following additions and modifications. *Sorbitol dehydrogenase*: 1.0 g D-sorbitol, 20 mg NAD, 25 mg NBT, 100 ml 0.05M tris-HCl buffer (pH 8.0), 5 mg PMS. *Mannose-6-phosphate isomerase*: 60 mg mannose-6-phosphate, 25 mg NADP, 20 mg MTT, 40 units G-6-PDH, 30 units PGI, 100 ml 0.5M tris-HCl buffer (pH 8.0), 5 mg PMS.

The abbreviations for the enzymes, as given in Table 1, are used to indicate the corresponding gene loci when the abbreviations are *italicized*. When more than one zone of activity exists for a given enzyme, a suffix has been added to the abbreviation to designate which zone is being considered. The zone of activity with the least migration is designated 1, the next is designated 2, and so on. The esterase zymogram has numerous zones of activity and only the zone with the greatest migration is considered in this study. For each locus, the most common allele in the Bodega Bay population of *Littorina scutulata* has been arbitrarily labelled 100. The other alleles are labelled in relation to this standard by addition or subtraction from 100 of the number of millimeters by which their migration differs from the standard.

Allelic frequencies in different populations of the two species of *Littorina* were compared by chi-square analyses of the observed allele numbers. Classes of alleles were combined whenever expected allele numbers were less than three, and an adjusted chi-square was calculated for comparisons with one degree of freedom. Results were further analyzed by measuring the degree of genetic similarity between populations, using the statistic *I* as defined by NEI (1972). Values of *I* range from 0 to 1, where a value of 1 indicates genetic identity.

RESULTS

Electrophoresis

The results of the ten enzyme assays for the two sibling species are summarized in Table 2. Sample sizes and allelic frequencies for each population are shown, where sample size is the number of alleles assayed. Of the ten loci examined, two (*Acph-2* and *Got*) are monomorphic, *i.e.*, all individuals possess the same allele. The remaining eight loci are polymorphic with the number of alleles per enzyme ranging from two in *Lap-2* to eight in *Pgi*.

The chi-square analyses indicate that *Littorina scutulata* and *L. plena* do, indeed, have characteristic allelic frequencies. The differences between sympatric populations of the two species are all highly significant ($P < 0.01$) at the *Est*, *Ldh*, *Pgi*, *Pgm*, and *Sdh* loci. The Newport Beach populations also differ significantly ($P < 0.01$) at the *Mpi* locus, and populations at three out of five localities tested show some difference at the *6-pgdh* locus ($P < 0.05$). Over all localities, the differences between *L. scutulata* and *L. plena* are significant ($P < 0.05$) in all between-site comparisons at the *Est*, *Ldh*, *Pgi*, and *Sdh* loci. The allelic frequencies of the two species also differ in a statistically significant manner in 18 of 20 between-site comparisons at the *Pgm* locus, in 5 of 20 comparisons at the *6-pgdh* locus, and in 5 of 20 comparisons at the *Mpi* locus ($P < 0.05$).

Genetic similarities between populations (Nei's *I*) are shown in Table 3 for all possible pairwise combinations. The average genetic similarity between the populations of *Littorina scutulata* is 0.962 ± 0.025 . The average genetic

Table 3

Genetic similarities (*I*) between pairs of *Littorina* populations.

<i>Littorina scutulata</i> populations					<i>Littorina plena</i> populations					
	SR	BB	SLO	NB		PA	SR	BB	SLO	NB
<i>Littorina scutulata</i>										
PA	0.9581	0.9413	0.9694	0.9010		0.6787	0.7249	0.6728	0.7421	0.7453
SR	—	0.9720	0.9736	0.9852		0.6740	0.7490	0.6837	0.7417	0.7586
BB	—	—	0.9752	0.9764		0.6207	0.6784	0.6314	0.6848	0.6978
SLO	—	—	—	0.9668		0.6650	0.7222	0.6815	0.7566	0.7566
NB	—	—	—	—		0.6858	0.7366	0.6816	0.7481	0.7544
<i>Littorina plena</i>										
PA	—	—	—	—		—	0.9640	0.9404	0.9363	0.9421
SR	—	—	—	—		—	—	0.9773	0.9554	0.9737
BB	—	—	—	—		—	—	—	0.9338	0.9704
SLO	—	—	—	—		—	—	—	—	0.9772

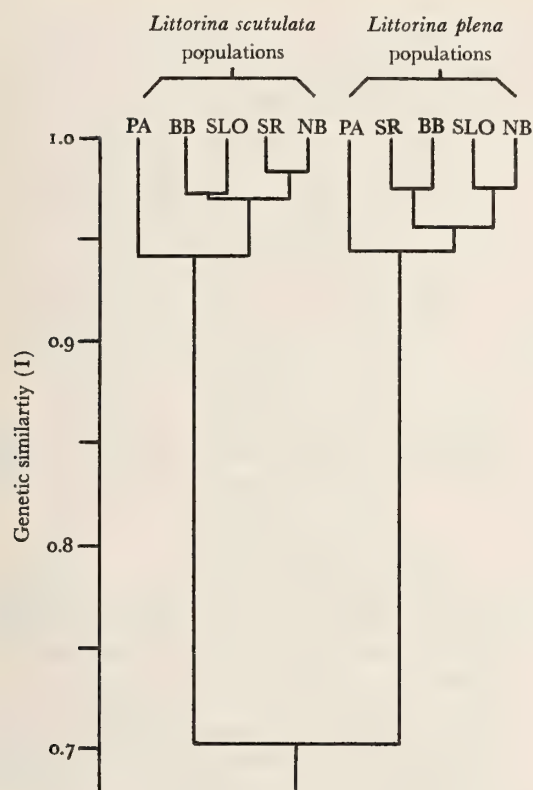


Figure 2

Dendrogram expressing levels of genetic similarity among *Littorina scutulata* and *Littorina plena* populations (UPGM cluster analysis)

similarity is likewise high for populations of *L. plena*. (0.957 ± 0.018). Measures of genetic similarity between populations of the two species, however, are consistently lower, averaging 0.707 ± 0.058 . The genetic similarities between all pairs of populations have also been converted into a dendrogram (Figure 2) using an unweighted pair group method of cluster analysis (SOKAL & SNEATH, 1963). Clearly, the ten populations fall into two groups, one consisting of the five *L. scutulata* populations and the other composed of the five *L. plena* populations. The degree of genetic differentiation between the two species is far greater than that within either.

Morphology

Consistent specific differences in the general morphology of egg capsules and penes exist between *Littorina scutulata*

and *L. plena* at all fifteen localities studied (Figure 3). Female *L. plena* produce planktonic egg capsules with two outer rims of nearly equal diameters, while males possess an attenuate penis with one large papilla and an elongated tip. Female *L. scutulata* spawn egg capsules with two rims of very different diameters, while males possess a somewhat truncate penis lacking papillae.

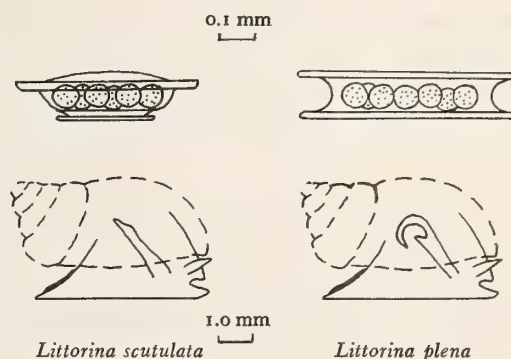


Figure 3

The planktonic egg capsule and penis morphology of *Littorina scutulata* and *Littorina plena*

The shell morphology of both species appears to vary with both habitat and geographic location. Furthermore, intraspecific variation often results in considerable interspecific overlap in any one shell character for sympatric populations of the two species. *Littorina plena* from exposed rocky shores near Bodega Bay become mature at shell lengths of 2-3 mm and grow to a maximum length of 11 mm. Most individuals have shells with 3-4 whorls. The interior of the aperture usually displays an amber band curving inward near the base of the shell. *L. scutulata* from the same shores become mature at lengths of 4-7 mm and reach lengths of 17 mm. Individuals possess shells with approximately 4-5 whorls that usually lack the amber band seen in *L. plena*. Shell color in both species is highly variable, ranging from black or dark purple to gray, green, or light brown. However, the shells of *L. scutulata* do tend to have more tessellations than those of *L. plena*.

The radular morphologies of *Littorina scutulata* and *L. plena* are typical of all Littorinidae (Figure 4). Radulae of both species stained in fuchsin and examined under a light microscope show numerous transverse rows of teeth, each row consisting of a single central or rachidian tooth flanked on each side by one lateral and two marginal teeth. Although the interspecific overlap is again large,

Table 4

Length/width ratios of the rachidian tooth of *Littorina scutulata* and *Littorina plena* from Bodega Bay. Approximately 30 measurements were made with an ocular micrometer at 400 \times and then averaged for each replicate radula. Length/width ratios were statistically independent of shell length in each species.

Species	n	Range of tooth lengths (microns)	Range of tooth widths (microns)	Length/width ratio \pm one standard deviation
<i>Littorina scutulata</i>	20	37.1 - 52.5	42.5 - 63.0	0.868 \pm 0.053
<i>Littorina plena</i>	20	10.6 - 34.3	10.6 - 32.0	0.990 \pm 0.084

Wilcoxon's two sample test: *Littorina scutulata* ratio \neq *Littorina plena* ratio; $P < 0.001$.

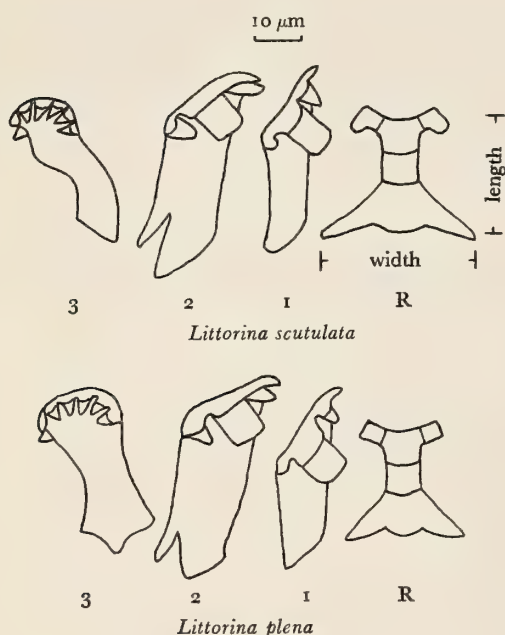


Figure 4

Radular teeth from one side of a transverse row
 R - rachidian; 1 - lateral; 2 - inner marginal
 3 - outer marginal

Bodega Bay populations of the two species differ significantly in the length to width ratio of the rachidian tooth (Table 4).

Taxonomy

GOULD (1849) described three species of *Littorina* from the west coast of North America which were subsequently synonymized under the name *L. scutulata* by Carpenter (1864). The type specimens for the three species kept at

the United States National Museum of Natural History were examined to clarify their taxonomic status.

Type Material and Type Localities

- Littorina scutulata* Gould: (Puget Sound, Washington)
 Holotype USNM 5640: length 12.43 mm, width 8.26 mm
 Paratype USNM 612308: length 8.97 mm, width 5.86 mm
- Littorina plena* Gould: (San Francisco, California)
 Lectotype USNM 5635: length 8.53 mm, width 5.42 mm
 Paralectotypes USNM 677096: both males; length 8.34 mm, width 5.55 mm; length 6.42 mm, width 4.27 mm
- Littorina lepida* Gould: (Puget Sound, Washington)
 Lectotype USNM 5637, length 9.11 mm, width 6.12 mm
 Paralectotype USNM 677095, length 8.11 mm, width 5.15 mm

Measurements are given with shell width perpendicular to shell length.

The holotype of *Littorina scutulata* is large and highly tessellated. This specimen probably represents a group distinct from *L. plena*, and we suggest that *L. scutulata* Gould, 1849, be retained as a valid name for the species as established in this investigation.

The paralectotypes of *Littorina plena* contained intact bodies within the shells. The bodies were rehydrated, removed, and positively identified as male *L. plena* by the morphology of their penes. On the basis of this identification, we propose that the species name *L. plena* Gould, 1849, be resurrected to define the second sibling species (even though other type material may prove to be a mixture of species).

At this time, the type material of *Littorina lepida* cannot be reliably assigned to either *L. scutulata* or *L. plena*.

Voucher specimens of *Littorina scutulata* have been obtained from the exposed rocky shores northwest of Horseshoe Cove on the biological reserve of the University of California, Bodega Bay, California. In addition to the Bodega Bay location, voucher specimens of *L. plena* have been obtained from the rip-rap on the south side of

the Berkeley Marina and from rocky outcrops at the north end of Baker's Beach, San Francisco, California. These specimens have been deposited at the National Museum of Natural History (USNM), the California Academy of Sciences (CASIZ), and the Natural History Museum of Los Angeles County (LACM).

Littorina scutulata voucher specimens and locality:

USNM 803490, CASIZ 024458, LACM 67755: Bodega Bay, California (38°19'00" N; 123°04'16" W)

Littorina plena voucher specimens and localities:

USNM 803491, CASIZ 024456, LACM 67756: Bodega Bay, California (38°19'00" N; 123°04'16" W)

USNM 803492, CASIZ 024457, LACM 67757: Berkeley, California (37°51'18" N; 122°18'50" W)

USNM 803493, CASIZ 024455, LACM 67758: San Francisco, California (37°48'21" N; 122°28'40" W)

DISCUSSION

The taxonomy of several *Littorina* species has been recently revised to include the presence of additional, morphologically similar species. Sympatric sibling species of *Littorina* are now recognized on the Hawaiian Islands (WHIPPLE, 1965), among the West Indian fauna (BORKOWSKI & BORKOWSKI, 1969), and on British shores (HELLER, 1975; HANNAFORD ELLIS, 1979). *Littorina scutulata* and *L. plena* represent still another example of co-existing species of littoral gastropods possessing very similar morphological and ecological attributes.

The electrophoretic data presented in this study indicate reproductive and genetic separation, if not total isolation, between *Littorina scutulata* and *L. plena*. Within either species, very little genetic differentiation appears to have occurred between populations as far apart as San Diego and Point Arena. Interspecific comparisons, however, consistently show significant differences in allelic frequencies between *L. scutulata* and *L. plena*, at levels exceeding the genetic differentiation measured by WILKINS & O'REGAN (1980) for three species of the British *L. saxatilis* species complex and by WARD & WARWICK (1980) for *L. arcana* Hannaford Ellis, 1978, and *L. rudis* (Maton, 1797). Such biochemical evidence indicates that *L. scutulata* and *L. plena* are two separate reproductive and genetic entities worthy of species status.

Various aspects of the reproductive biology of *Littorina* are often species-specific traits, and differences in these traits can be strong evidence of separate sibling species. Mode of reproduction (HELLER, 1975), morphology of genitalia (WHIPPLE, 1965; HELLER, 1975; GOODWIN & FISH, 1977), and characteristics of spawn (WHIPPLE, 1965; BORKOWSKI & BORKOWSKI, 1969) are used to distinguish between snails whose identities based on shell

morphology are ambiguous. MURRAY (1979) notes for *L. scutulata* and *L. plena* that females of each species spawn characteristic egg capsules; in addition, males display differences in penis morphology, differences similar to those which HELLER (1975) suggests may be of importance in species recognition and ethological isolation of British *Littorina*. Although reproductive attributes have been questioned as taxonomic characters in certain instances (BORKOWSKI, 1975; RAFFAELLI, 1979; CAUGANT & BERGERARD, 1980), the agreement of the biochemical data in this investigation with the dichotomy described by MURRAY (1979) indicates that the reproductive distinctions between *L. scutulata* and *L. plena* are reliable species discriminators.

In response to environmental clines, many species of *Littorina* exhibit considerable variation in morphological features (STRUSAKER, 1968; NEWKIRK & DOYLE, 1975; HYLLEBERG & CHRISTENSEN, 1977) to the extent that the taxonomic status of some populations has been in doubt (COLMAN, 1932; HUGHES, 1979; RAFFAELLI, 1979). *Littorina scutulata* and *L. plena* occupy a diversity of habitats ranging in degree of exposure from protected bays and estuaries to the exposed open coast, and both species show substantial intra-habitat as well as inter-habitat variation in shell and radular characters. Reliable separation of the two species on the basis of these morphological traits is likely to depend upon the particular populations examined and may involve a combination of several shell or radular characters, or both.

In such cases where regional and intra-population variation in morphology are great, the application of electrophoretic techniques produces results which are less affected by factors other than the genotype of the individual. In this study, the biochemical genetic evidence supports subtle morphological differences as well as the reproductive distinctions previously detailed by MURRAY (1979) as indicators of two biological species. These results confirm the presence of the sympatric sibling species, *Littorina scutulata* and *L. plena*.

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Gametogenesis and Spawning in a Population of *Geukensia demissa*

(Pelecypoda : Mytilidae)

from Westport, Connecticut

BY

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(2 Plates; 1 Text figure)

INTRODUCTION

THE RIBBED MUSSEL, *Geukensia demissa* (= *Modiolus demissus*) is a dominant component of the *Spartina alterniflora* zone in the salt marsh communities of the east coast of North America. Considerable attention has been given to the behavioral and physiological adaptations which make this species a successful intertidal inhabitant (KANWISHER, 1955; WELLS, 1961; LENT, 1969). However, its reproductive ecology has remained largely unstudied.

The scanty evidence available suggests a summer spawning period for this species along the Atlantic coast of North America. McDUGALL (1943) reports the occurrence of *Geukensia demissa* spat in August through October in Beaufort, North Carolina. In Malpeque Bay, Prince Edward Island, Canada, SULLIVAN (1948) found larvae of this species present from mid-July to August. KUENZLER (1961) reports that a population of *G. demissa* from Sapelo Island, Georgia spawns during the late summer. However, his method for determining this is not given, nor does he provide any specific information on the gametogenic cycle itself.

The present study was designed to 1) define and categorize the sequence of gametogenic development based on microscopic examination of gonadal tissue and 2) determine the frequency and duration of the spawning cycle in a natural setting.

MATERIALS AND METHOD

Geukensia demissa were collected from the westernmost end of a salt marsh located at Sherwood Island State Park

on Long Island Sound, Westport, Conn., U.S.A. (41°07' N; 73°19' W) from June 1979 to December 1980. Sample sizes varied from 7 to 25 mussels, 31.9-114.6 mm shell length. A total of 354 mussels were examined.

In the laboratory the mussels were numbered, their maximum length (± 0.1 mm) determined and sections of both the visceral mass and the mantle with the gonads were removed and fixed in 10% buffered formalin during the first 15 months of study. The tissues were then prepared for histological examination according to the method described by Brousseau (1978). A microscopic examination was made of both the mantle and visceral mass gonadal tissue before assigning each individual to the appropriate category of gonadal condition. Since there was no significant difference in gonadal development in different sections of gonad (Table 1) only the mantle tissue was excised during the last 4 months of the study. The results are based on the developmental condition of the mantle tissue in all individuals examined. Photomicrographs of representative stages of the male and female reproductive cycle were taken with a Zeiss microscope at 125X magnification using a 35 mm camera. Panatomic X ASA 32 film was used.

RESULTS

Categories of Gonad Condition

The following descriptions of the male and female developmental stages divide the reproductive process (either spermatogenesis or oogenesis) into distinct phases. The criteria used are based solely on morphological observa-

Table 1

Numbers of mussels, *Geukensia demissa*, reported in each reproductive category based on the condition of the mantle (MAN) and visceral mass (VM) tissue. Sample sizes are given in parentheses.

Sampling date	MAN					VM				
	Indiff.	Develop.	Ripe	Partially spawned	Spent	Indiff.	Develop.	Ripe	Partially spawned	Spent
5 June 1979 (18)	—	—	2	15	1	—	—	2	16	—
18 July 1979 (7)	—	—	—	5	2	—	—	—	6	1
15 August 1979 (15)	—	—	5	9	1	—	—	3	12	—
12 September 1979 (21)	—	—	1	16	4	—	—	2	13	6
10 October 1979 (22)	2	—	—	3	17	3	—	—	2	17
8 November 1979 (20)	11	1	—	—	8	16	—	—	—	4
12 December 1979 (22)	16	—	—	—	6	17	1	—	—	4
10 January 1980 (11)	7	—	—	—	4	9	—	—	—	2
29 February 1980 (13)	11	—	—	—	2	12	—	—	—	1
26 March 1980 (16)	15	1	—	—	—	15	1	—	—	—
14 April 1980 (12)	11	1	—	—	—	12	—	—	—	—
13 May 1980 (15)	—	15	—	—	—	—	15	—	—	—
7 June 1980 (17)	—	2	13	2	—	—	2	11	4	—
15 July 1980 (16)	—	—	—	16	—	—	—	2	14	—
4 August 1980 (16)	—	—	—	16	—	—	—	2	14	—

tions. Categories comparable to those already in use for other species have also been used in this study where appropriate (ROPES & STICKNEY, 1965; BROUSSEAU, 1978, for *Mya arenaria*; PORTER, 1964; KECK *et al.*, 1975, for *Mercenaria mercenaria*; BROUSSEAU, 1981, for *Petricola pholadiformis*).

Developmental Stages of the Male

Indifferent Stage

The interfollicular space dominates, consisting almost entirely of large vacuolated fat cells. Follicles, empty except for occasional residual spermatozoa and phagocytes, are scattered throughout the gonad. There were no pycnotic cells or multinucleated non-pycnotic cysts present in the follicles (Figure 1a).

Developing Stage

The spermatogenic cells begin to proliferate around the follicle walls. A wide, centripetal band of spermatogonia, spermatocytes and spermatids develops. The interfollicular connective tissue decreases with fewer large vacuolated fat cells being produced. The spermatids then differentiate into spermatozoa which appear as a dense mass in the lumen of the follicle (Figure 1b).

Ripe Stage

The mass of mature spermatozoa increases in volume and the individual cells arrange themselves into bands with tails pointing toward the center of the lumen. Occasionally, the spermatozoa lose continuity with the rest of the cell contents forming a "plug" (Figure 1c).

Explanation of Figure 1

Photomicrographs of gonadal stages of the male ribbed mussel, *Geukensia demissa*. a) indifferent male ($\times 125$), 12 December 1979; b) developing male ($\times 125$), 13 May 1980; c) ripe male ($\times 125$), 15 July 1980; d) partially spawned male ($\times 125$), 18 July 1979; e) spent male ($\times 125$), 12 September 1979

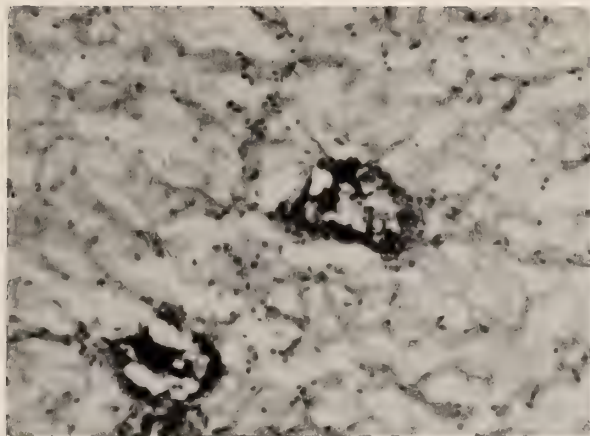


Figure 1a

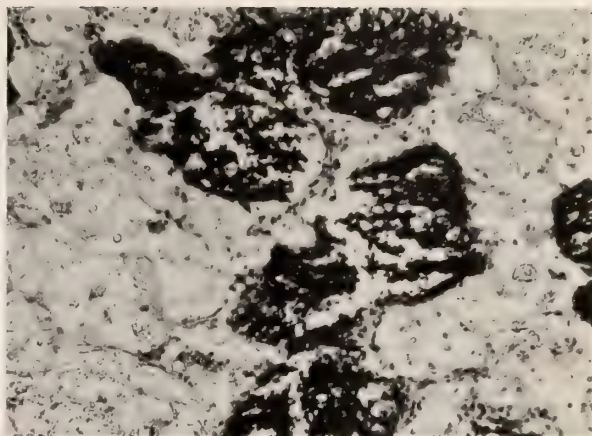


Figure 1b

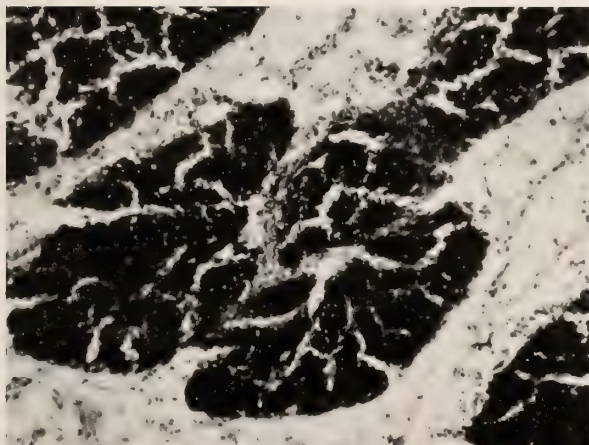


Figure 1c

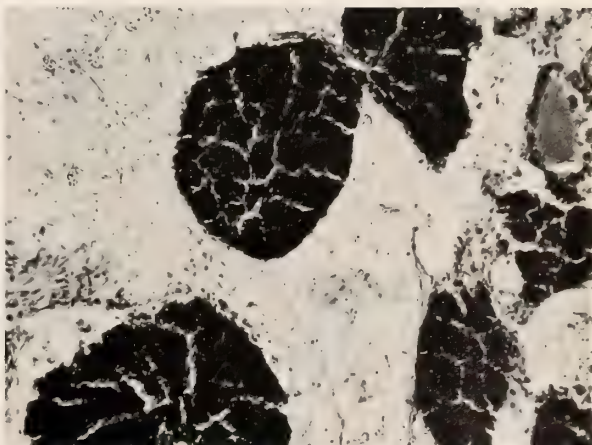


Figure 1d

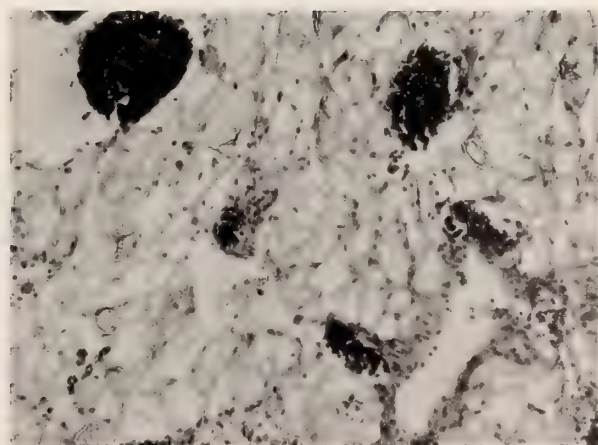


Figure 1e

Partially Spawned Stage

There is a marked decrease in the number of spermatozoa filling the lumen with most follicles empty or emptying (Figure 1d).

Spent Stage

In totally spawned males a few residual sperm are visible but the majority of follicles are empty. Spermatocytes are rare (Figure 1e).

Developmental Stages of the Female

Indifferent Stage

The interfollicular space dominates, consisting almost entirely of large vacuolated cells. The follicles are empty except for occasional residual free oocytes (Figure 2a).

Developing Stage

Oocytes become more noticeable along the follicle walls, increasing in size and number. The developmental phase is a continuous process involving a proliferation and maturation of the oocytes, with an accompanying reduction in interfollicular connective tissue. The developing oocytes which begin as hemispherical or cylindrical cells attached to the wall of the follicle become enlarged spherical cells, 30 to 40 μm in diameter as maturity approaches (Figure 2b).

Ripe Stage

Ripe females are characterized by the presence of large, round oocytes 65 to 70 μm in diameter, some of which are attached to the follicular wall by slender stalks. Others appear as free oocytes in the lumen of the follicle. There is a very prominent eccentrically placed nucleolus visible within the nucleus (Figure 2c).

Partially Spawned Stage

There is a noticeable reduction in the number of ripe oocytes present in the lumen and some follicles are completely devoid of sex cells (Figure 2d).

Spent Stage

Mussels which have recently undergone oogenesis can be recognized by the presence of a few unspawned oocytes in the lumen. These may be in varying degrees of cytolysis. Resumption of oogenic activity may be evident in some individuals (Figure 2e).

Reproductive Cycle

Reproductively active individuals (Developing, Ripe and Partially spawned) were encountered throughout the 19-month study except in December, January and February. The largest numbers of active individuals occurred in June and August of 1979 and May through August of 1980 (Figure 3). Gametogenesis began in March in both sexes but a large number of developing individuals were

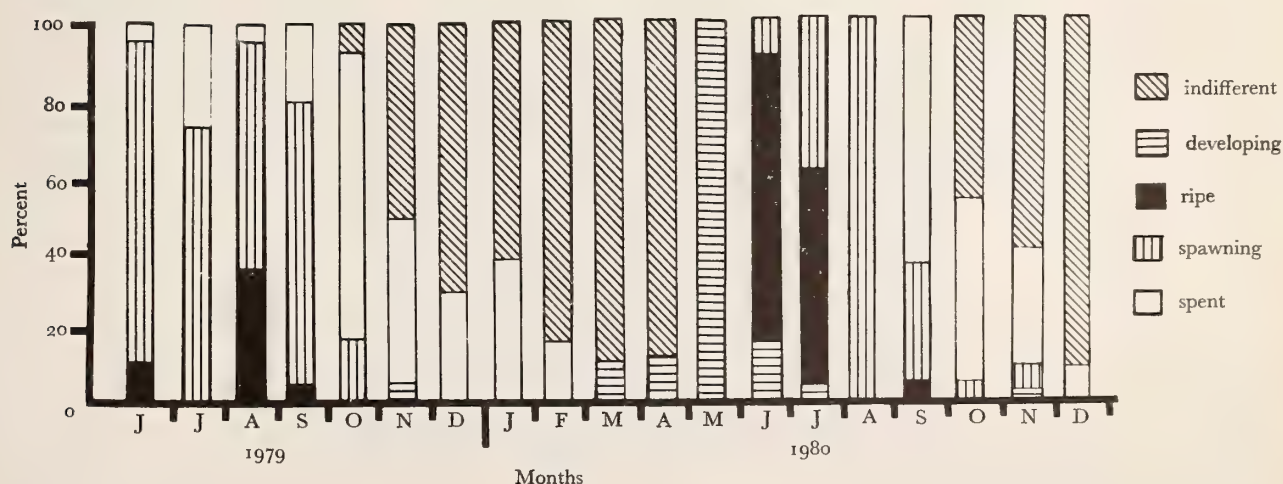


Figure 3

Proportions of *Geukensia demissa* population with gonads in each developmental phase during 1979-1980. Observations on males and females are combined

not apparent until May. Fully ripe individuals were observed June through September with over 60% of the mussels (both sexes) reported in a gravid condition in June and July of 1980. Discharge of eggs took place during the summer months. By mid-November over 60% of the mussels had completely spawned or returned to the indifferent condition.

In the population studied, the proportion of females in all size-classes ($N = 328$) did not differ significantly from one-half. Male and female gonads were distinguishable in all size-classes studied (> 31.9 mm). Although no protandry was observed, there was evidence of simultaneous hermaphroditism in some individuals. Seventeen of 258 mussels (7%) contained one type of sex cell in the mantle and the other in the visceral mass. Hermaphrodites were collected in all months except January, February and June and appeared to be undergoing normal gametogenic development.

DISCUSSION

Geukensia demissa is a dioecious pelecypod, the sexes of which are distinguishable only after examination of the gonads. COE (1943) includes the genus *Modiolus* in his description of the origin and early development of the gonad of pelecypod molluscs through sexual differentiation. However, there has been no discussion of gametogenic development in this species. Previous investigators have reported that *Geukensia demissa* is a strictly gonochoristic species (FRETTER & GRAHAM, 1964). Evidence here indicates otherwise. The low incidence of hermaphroditism exhibited by this species suggests *G. demissa* possesses stable gonochorism, a condition characterized by the presence of some hermaphrodites in a normally gonochoristic species.

The results of gonadal examinations indicate that *Geukensia demissa* from Westport, Connecticut spawn annually during the summer months (Figure 3). Other in-

vestigators also suggest a summer spawning for this species. In their review of reproductive cycles of marine invertebrates (GIESE & PEARSE, 1974), they concluded that, in general, the reproductive cycle of marine bivalves in colder environments tends to be short and to occur during the warmer months of the year, whereas those from warmer waters are extended, and less likely to show pronounced seasonality (Orton's Rule). Empirical evidence lends substantial support to Orton's second hypothesis. In North Atlantic species, spawning usually occurs during the warmer months of the year (SASTRY, 1979). In addition to *Geukensia demissa* studied here this includes such notable North American shallow water pelecypods as *Mya arenaria* (ROPES & STICKNEY, 1965; BROUSSEAU, 1978), *Mercenaria mercenaria* (PORTER, 1964; KECK *et al.*, 1975), *Macoma balthica* (GILBERT, 1978), *Crassostrea virginica* (LOOSANOFF, 1937), *Spisula solidissima* (ROPES, 1968), *Mulinia lateralis* (CALABRESE, 1970) and *Aequipecten irradians* (SASTRY, 1970).

Considerably less information exists, however, on the presence of latitudinal differences in the duration and frequency of the spawning cycle. Information available on *Mya arenaria* (ROPES & STICKNEY, 1965; BROUSSEAU, 1978), *Macoma balthica* (GILBERT, 1978) and *Mercenaria mercenaria* (PORTER, 1964 cited in ROPES, 1968) indicates that spawning in widely separated populations of these species occurs at different times and with varying frequency. However, there is no general agreement concerning the generality of Orton's Rule (GIESE & PEARSE, 1974). Information on the spawning cycle of *Geukensia demissa* from Georgia (KUENZLER, 1961) suggests that it may not exhibit an extended breeding pattern at the southern limits of its range, making it yet another exception to Orton's Rule. Only after more information becomes available, however, will it be possible to determine if the annual spawning pattern reported for *G. demissa* from Westport, Connecticut is replaced by a multiannual one in the southern portion of its range.

Explanation of Figure 2

Photomicrographs of gonadal stages of the female ribbed mussel, *Geukensia demissa*. a) indifferent female ($\times 125$), 12 December 1979; b) developing female ($\times 125$), 13 May 1980; c) ripe female ($\times 125$), 7 June 1980; d) partially spawned female ($\times 125$), 12 September 1979; e) spent female ($\times 125$), 12 September 1979

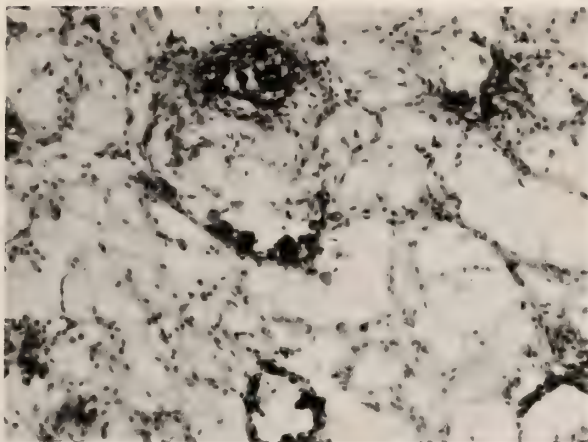


Figure 2a

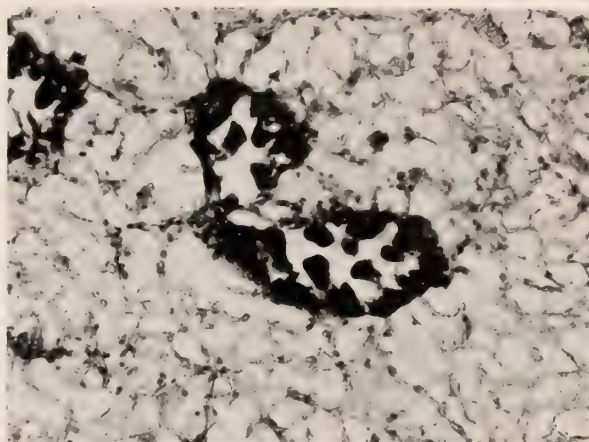


Figure 2b



Figure 2c

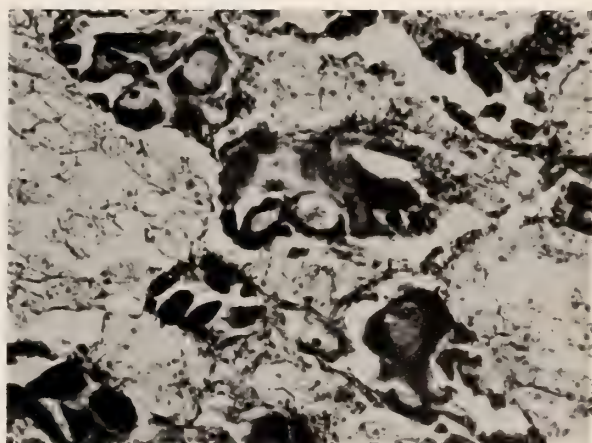


Figure 2d

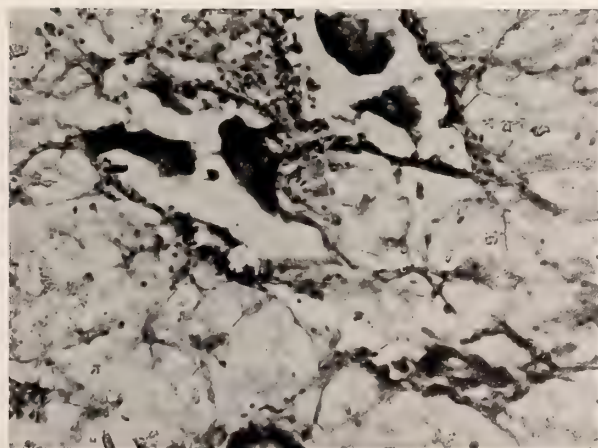


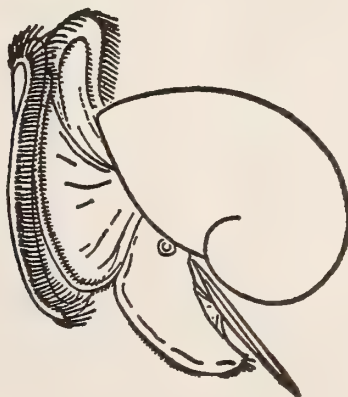
Figure 2e

SUMMARY

A population of *Geukensia demissa* in Long Island Sound, Westport, Connecticut was studied for 19 months to determine the sequence of gametogenic development of gonadal tissue and the frequency and duration of the spawning cycle under natural conditions. This population was observed to spawn annually in June-August. Sexes were distinguishable in all individuals studied (>31.9 mm shell length). A low incidence of simultaneous hermaphroditism suggests that *Geukensia demissa* is a stable gonochoric species. No evidence of protandry was observed. Sex ratios of *G. demissa* 31.9-114.6 mm shell length did not differ significantly from 1:1. Photomicrographs of the gametogenic cycles of both male and female mussels are included.

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The Early Development of Two Ovulid Snails, *Simnia aequalis* and *Simnia barbarensis*

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(1 Plate; 4 Text figures)

INTRODUCTION

MEMBERS OF THE GASTROPOD FAMILY Ovulidae are distributed throughout the world seas; however, they are most concentrated on the coasts of Australia, the Philippines, and Japan. Very few species occur sympatrically (CATE, 1969), and they are always found living on cnidarian hosts, usually alcyonarians (ABBOTT, 1968; CATE, 1969, 1973; HYMAN, 1967). The colors of the shells tend to blend with their hosts, being purple on purple gorgonians and yellow on yellow gorgonians (HYMAN, 1967; KEEN, 1971; OSBURN, 1885). The mantle covering the smooth shell also blends with the host and may bear small white projections which resemble host polyps (ABBOTT, 1968; PATTON, 1972; THEODOR, 1967). The taxonomy of this family has been revised many times (CATE, 1969, 1973, 1974; SCHILDER, 1968, 1971) and is currently in a state of confusion; it is based on shell morphology and coloration in adults, which is highly variable depending on age and the specific host of an individual.

Many species of prosobranchs (including all members of the family Ovulidae) lay their eggs in capsules; however, few researchers (CROFTS, 1937; ØSTERGAARD, 1950) have described the early development which occurs within these capsules. The only ovulid to be raised through its entire life cycle in the laboratory is *Neosimnia acicularis*. ADAMS (1968) raised *N. acicularis* through two generations and described its late development (pelagic). Late development has been examined in two other ovulids, *Simnia patula* and *Simnia spelta*. LEBOUR (1932) and THIRIOT-QUIÉVREUX (1967) each obtained estimates of length of

larval life, growth measurements, and developmental descriptions from planktotrophic larvae collected in plankton tows and maintained for short periods of time in the laboratory.

Simnia aequalis (Sowerby, 1887) lives on the gorgonian *Lophogorgia rigida* in the northern Gulf of California. *Simnia barbarensis* (Schilder, 1941) lives on the sea pens, *Acanthoptilum gracile*, *Ptilosarcus gurneyi*, and on the gorgonian, *Lophogorgia chilensis* in Southern California (Los Angeles County Natural History Museum collection and James Vallee, personal communication). The only information available on these two ovulids are the shell descriptions in BERRY (1916), CATE (1969, 1973), and SOWERBY (1848).

The objectives of this study were to describe the development of *Simnia aequalis* and *Simnia barbarensis* within egg capsules and immediately after hatching, to compare the development of *S. aequalis* and *S. barbarensis* to the development of other species previously described, and to discuss the significance of larval structures as taxonomic characters for the family Ovulidae.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE OF ADULT ANIMALS

Simnia aequalis were collected at the mouth of Estero Morua, located approximately five km south of the University of Arizona-University of Sonora Environmental Research laboratory in Puerto Peñasco, Sonora, Mexico (31.20° N; 113.35° W). *Simnia aequalis* is distributed from Puertecitos to San Felipe in Baja California, Mexico, and

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from Guaymas to Bahía de Adair in Sonora, W. Mexico (CATE, 1973). Water temperatures at Puerto Peñasco range from 15°C to 30.6°C (ROBINSON, 1973). Specimens along with their gorgonian hosts, *Lophogorgia rigida*, were collected on extreme low tides in September 1978 and January 1979. *S. aequalis* and their host gorgonians were maintained in recirculating natural seawater systems at $14 \pm 1^\circ\text{C}$. Each gorgonian colony was checked daily for newly deposited egg masses.

Simnia barbarensis were collected at depths of 4.6 to 9.1 m in the main exit channel of Mission Bay, California, U.S.A. (32.46°N; 117.14°W) on the sea pen *Acanthoptilum gracile*, in January 1979; *A. gracile* were also collected in February and June 1979 as food for *S. barbarensis*. The distribution of *S. barbarensis* is not known; however, they were previously collected in San Pedro Bay, Santa Barbara, and Morro Bay, California (CATE, 1973). Water temperatures in Mission Bay range from 13.9°C to 20.6°C (U.S. National Weather Service). *Simnia barbarensis* were maintained in recirculating natural seawater at $11 \pm 1^\circ\text{C}$. These snails were offered fresh *A. gracile* weekly and each *A. gracile* colony was checked daily for deposited egg masses.

REARING CONDITIONS

Egg masses were maintained in 250 mL seawater in Pyrex beakers with loose glass lids. Each beaker was washed and autoclaved before its use to prevent contamination (ALLEN & NELSON, 1908). To avoid possible sewage contamination, all seawater was collected at least 8 km off the Southern California coast in the Catalina channel. Incoming seawater was UV treated to prevent bacterial and fungal growth (LOOSANOFF & DAVIS, 1963) and filtered to remove suspended particles.

Larvae of both species were grown at $14 \pm 1^\circ\text{C}$ and $18 \pm 3^\circ\text{C}$. Two temperatures were used to determine which produced faster growth and a greater rate of survival.

All cultures were maintained under continuous illumination. PILKINGTON & FRETTER (1970) found that larvae

grew faster under constant illumination than under alternating 12 h periods of light and dark.

T-tests were performed to determine if there was a significant difference ($\alpha < 0.05$) in: (1) the sizes of *Simnia aequalis* and *Simnia barbarensis* larvae at each developmental stage, (2) the rate of development of *S. aequalis* and *S. barbarensis* at the same temperature, and (3) the length of development of each species at 14°C and 18°C .

OBSERVATION TECHNIQUES

Egg masses were examined daily under a dissecting microscope and the developmental stage of the larvae was recorded. When at least two capsules within one egg mass contained larvae which had progressed to the next larval stage, that egg mass was declared to have reached the next stage. Larval measurements were made using an ocular micrometer mounted on a compound microscope. Drawings were made with the aid of a camera lucida on either a dissecting or compound microscope. Photomicrographs were also taken of veligers of both species with a 35 mm camera mounted on a Zeiss microscope (50.4 magnification). Scanning Electron Microscope (I.S.I. SEM-II, Model SMSM) micrographs were taken of veliger shells at hatching. Specimens were prepared by soaking in 70% bleach for 2 days to dissolve the tissue and transferred to the SEM stub in a drop of water, where they were attached with polylysine. The water was then removed and the specimens were allowed to dry for 2 days.

RESULTS

EGG CAPSULES

Simnia aequalis laid their eggs in round gelatinous capsules on branches of *Lophogorgia rigida*. An egg mass consisted of multiple capsules laid at one time and joined by a colorless, transparent, fibrous membrane (Figure 1). Branches of *L. rigida* were not damaged by an egg mass; following hatching, the mass fell off the gorgonian and previously covered polyps resumed feeding. Capsules were

Table 1

Characteristics of egg masses of *Simnia aequalis* and *Simnia barbarensis*.

Species	Mean number of egg capsules per egg mass	Mean number of eggs per capsule	Mean volume of egg capsule	Volume available to one egg within a capsule
<i>Simnia aequalis</i>	17.7 ± 0.95^1 (53) ²	198.4 ± 27.86 (5) ³	0.209 ml (8) ³	0.0011 ml
<i>Simnia barbarensis</i>	47.6 ± 7.29 (16)	634.2 ± 8.60 (5)	0.550 ml (8)	0.00087 ml

¹± Standard error.

²No. of egg masses examined.

³No. of egg capsules examined.

Abbreviations used in Figures

Ab - Albumen
AM - Albumen membrane
AP - Apical plate
AT - Apical tuft

Dg - Digestive gland
E - Egg
F - Foot
FM - Fibrous layer of membrane
VP - Velum primordium

M - Mouth
O - Operculum
S - Shell
SP - Shell primordium

St - Statocyst
Tr - Trochoblast
V - Velum
VC - Velar cilia

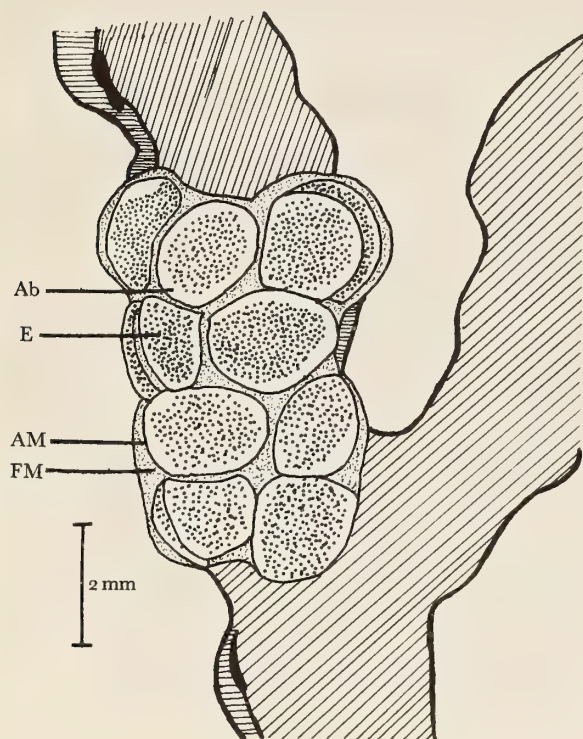


Figure 1

Egg capsules
of *Simnia aequalis* on the gorgonian *Lophogorgia rigida*

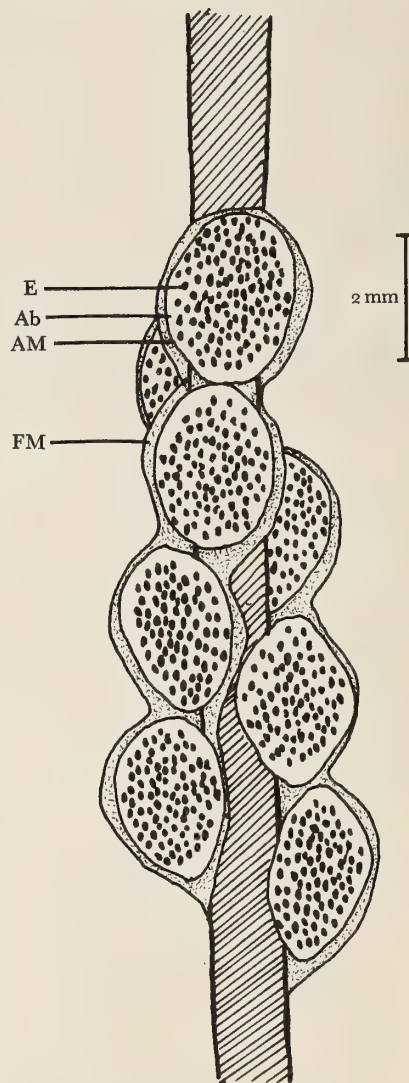


Figure 2

Egg capsules
of *Simnia barbarensis* on the skeletal axis of *Acanthoptilum gracile*

white and transparent, allowing eggs to be seen through the albumen membrane. Of 53 egg masses examined, the number of capsules varied between 6 and 40 ($\bar{X} = 17.7$). Mean volume of egg capsules was 0.209 mL and the volume available to one egg within a capsule was 0.0011 mL. The number of eggs per capsule varied between 131 and 280 (Table 1). *Simnia aequalis* laid eggs throughout the year in the laboratory, while gorgonians with egg masses were collected in September, January, March, and April in the field.

Simnia barbarensis eggs were laid in oval capsules on the stripped skeletal axis of *Acanthoptilum gracile*. Cap-

sules were also joined by fibrous membranes in the form of an egg mass (Figure 2). Capsules were white and transparent. Of 16 egg masses examined, the number of capsules varied between 11 and 107 ($\bar{X}=47.6$). Mean capsule volume was 0.55 mL, and the volume available to one egg within a capsule was 0.00087 mL. The number of eggs per capsule varied between 610 and 651 (Table 1). In the laboratory, *S. barbarensis* laid eggs for a seven month period beginning in February and ending in late August. Field collections of sea pens were made in January, February, and June; egg masses were present only in June. *Simnia barbarensis* eggs were more crowded within egg capsules (no. eggs per mL) than those of *Simnia aequalis* (no. eggs per mL) (Table 1).

LARVAL DEVELOPMENT

Simnia aequalis and *Simnia barbarensis* passed through 4 developmental stages inside their egg capsules. In the first stage, eggs underwent cleavage and passed through the blastula and gastrula stages. Eggs of both species were opaque white during this period. There was no noticeable movement and the eggs were suspended in albumen.

Following gastrulation, early trochophores appeared 7.9 days (\bar{X}) after laying in *Simnia aequalis* and 11.2 days (\bar{X}) after laying in *Simnia barbarensis* at 14°C (Table 2). *Simnia barbarensis* were significantly larger than *S. aequalis* at this stage. Mean length and width were 129.7 μm and 113.5 μm , respectively, in *S. aequalis*, and 142.5 μm and 119.8 μm in *S. barbarensis* (Table 3). Larvae of both species were oval, whitish, transparent balls which were larger than the gastrula stage. If a capsule was broken, releasing the trochophores, they turned opaque white. Early trochophores possessed an apical plate and tuft (Figure 3). Larvae appeared to move continuously. Larvae of both species were very similar, except for the larger trochoblasts in *S. aequalis* (Figures 3A and C).

Early trochophores developed into late trochophores within 3 to 4 days. Although *Simnia barbarensis* were larger than *S. aequalis* in the late trochophore stage, this difference was non-significant. Mean length and width were 124.9 μm and 101.09 μm , respectively, in *S. barbarensis* and 122.3 μm and 91.6 μm in *S. aequalis* (Table 3). Late trochophores were opaque white and were more elongate and narrower than early trochophores. As the velum began to develop (Figure 4), and both the shell and

Table 2

Mean time, in days, to reach each developmental stage.

Temperature °C	Species	Early trochophore	Late trochophore	Veliger	Time to hatching
14	<i>Simnia aequalis</i>	7.9 \pm 0.22 ⁴ (14) ⁵	11.1 \pm 0.30 (14)	15.9 \pm 0.38 (12)	24.6 \pm 1.08 (11)
	<i>Simnia barbarensis</i>	11.2 \pm 0.65 (6)	15.4 \pm 0.75 (5)	20.5 \pm 0.84 (6)	26.3 \pm 2.19 (3)
18	<i>Simnia aequalis</i>	6.0 \pm 0.31 (15)	8.4 \pm 0.31 (14)	11.7 \pm 0.45 (14)	17.6 \pm 1.09 (12)
	<i>Simnia barbarensis</i>	8.0 \pm 0.78 (8)	11.0 \pm 0.98 (7)	13.7 \pm 0.88 (6)	19.7 \pm 1.43 (6)

⁴ \pm Standard error.

⁵No. of egg masses examined.

Table 3

Dimensions of larval stages of *Simnia aequalis* and *Simnia barbarensis*.

Species	Early trochophores		Late trochophores		Veliger shells	
	Length (in μm)	Width (in μm)	Length (in μm)	Width (in μm)	Length (in μm)	Width (in μm)
<i>Simnia aequalis</i>	129.7 \pm 6.57 ⁶ (6) ⁷	113.5 \pm 5.14 (6)	122.3 \pm 4.46 (7)	91.6 \pm 2.68 (7)	123.8 \pm 2.12 (25)	96.8 \pm 2.32 (25)
<i>Simnia barbarensis</i>	142.5 \pm 2.50 (4)	119.8 \pm 3.40 (4)	124.9 \pm 4.52 (10)	101.9 \pm 5.44 (10)	144.4 \pm 1.52 (16)	107.0 \pm 2.12 (16)

⁶Standard error.

⁷Number of larvae measured.

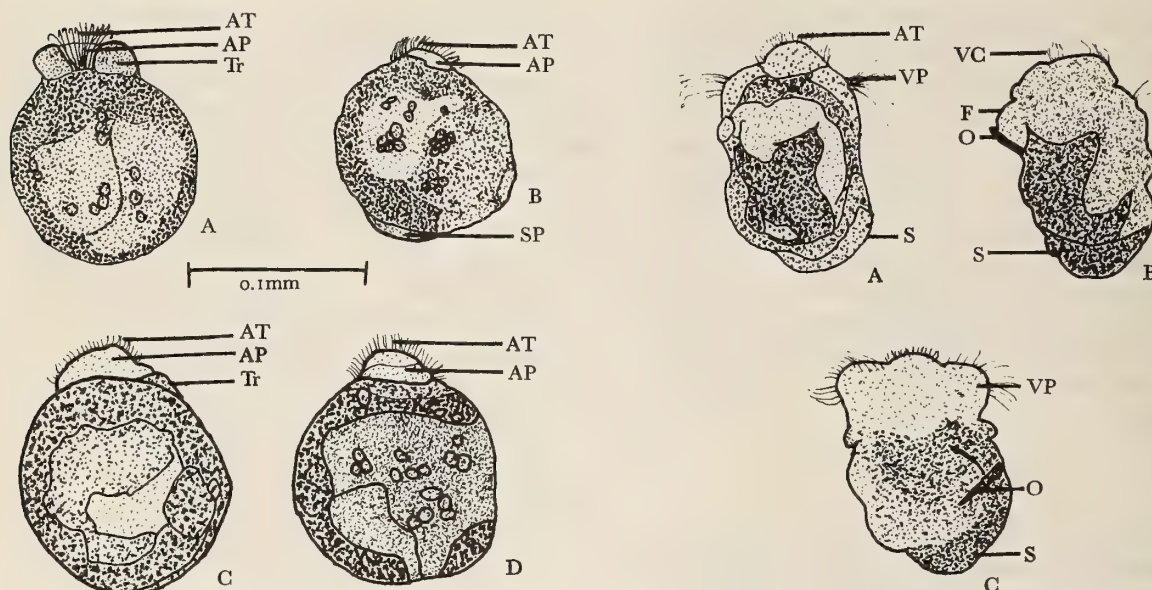


Figure 3

Early trochophores
of *Simnia aequalis* (A, B) and *Simnia barbarensis* (C, D)

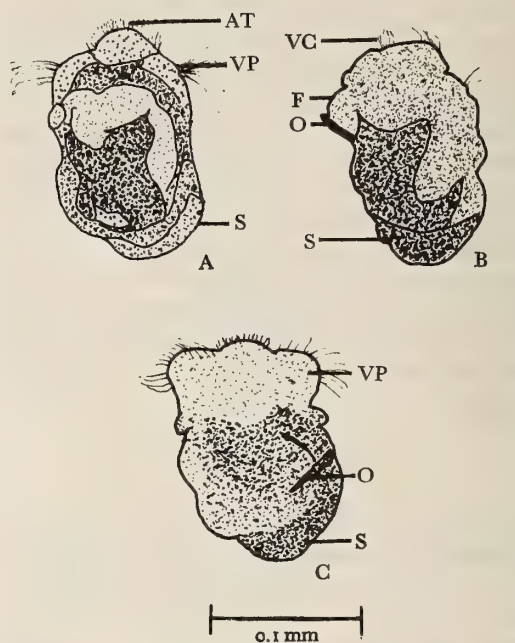


Figure 4

Late trochophores
of *Simnia aequalis* (A, B, C) and *Simnia barbarensis* (D, E)

operculum developed, velar and apical cilia became evident. Late trochophores were very similar in both species.

Veligers of both species were distinguished by the presence of a developed velum and a light pink shell, which darkened to a pinkish-brown before the larva left the capsule. The veliger stage began 15.9 days (\bar{X}) after laying in *Simnia aequalis* and 20.5 days (\bar{X}) after laying in *Simnia barbarensis* at 14°C (Table 2). The pink shell was transparent and the digestive gland could be seen through the shell. The foot and body of veligers were white and had two transparent, round, ciliated velar lobes. Two statocysts were clearly evident through the transparent operculum on the bottom of the foot (Figure 5).

Veligers left their egg capsules through a round, off-centered hole. This exit hole appeared to be a weak point on the capsule, which was opened by the force of veligers as they continually bumped into the capsule wall. Veligers hatched 24.6 days (\bar{X}) after laying in *Simnia aequalis* and

26.3 days (\bar{X}) after laying in *Simnia barbarensis* at 14°C (Table 2). At hatching, the larval shells of *S. aequalis* had a mean length and width of 123.8 μm and 96.8 μm , respectively, while those of *S. barbarensis* were 144.4 μm and 107.0 μm (Table 3). Veligers of *S. barbarensis* and *S. aequalis* were identical except for their size, with *S. barbarensis* veligers being significantly larger.

Explanation of Figures 5 to 7

Figure 5: A-D, Veligers of *Simnia barbarensis*; E-H, veligers of *Simnia aequalis*. All photomicrographs of veligers were taken at the same magnification

Figure 6: A, Veliger shell of *Simnia barbarensis*
B, Veliger shell of *Simnia aequalis*

× 430
× 480

Figure 7: A, Veliger shell of *Simnia barbarensis*
B, Veliger shell of *Simnia aequalis*

× 400
× 470

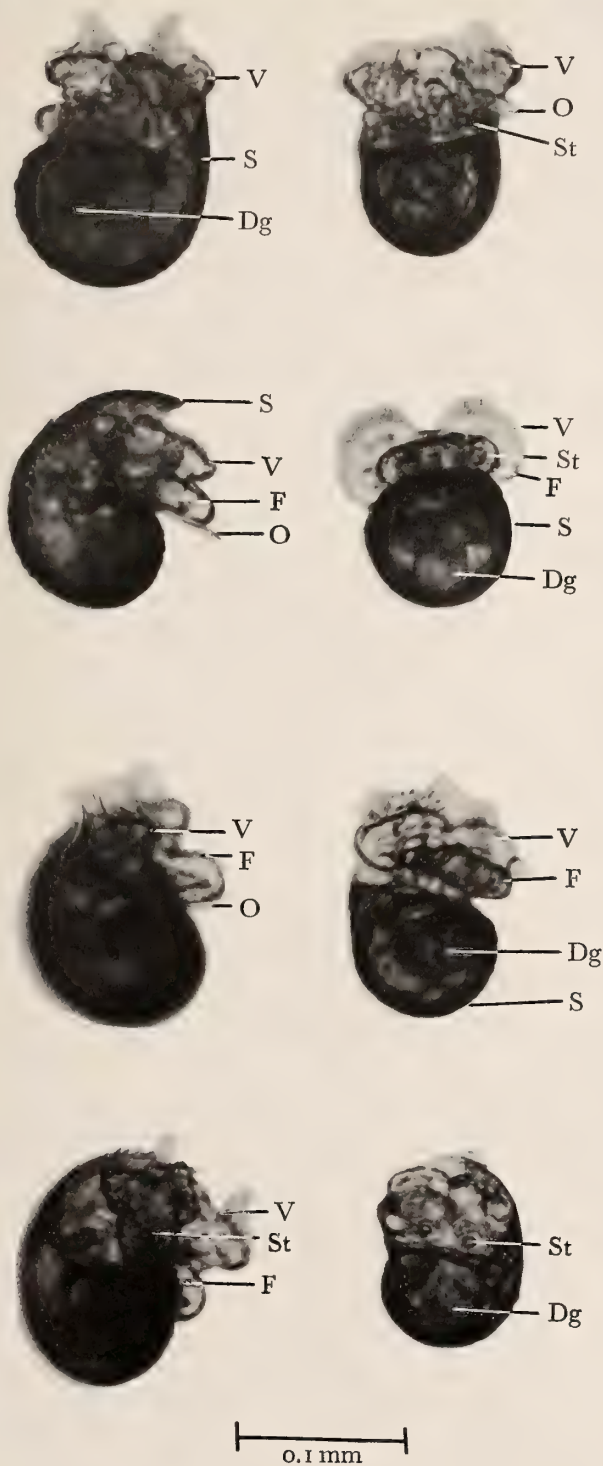
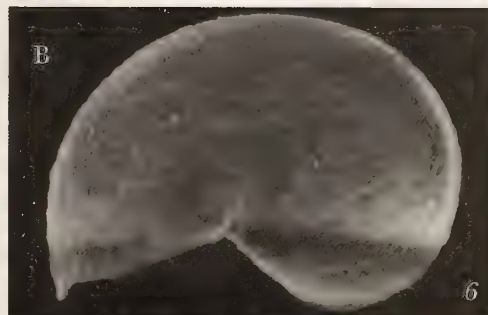
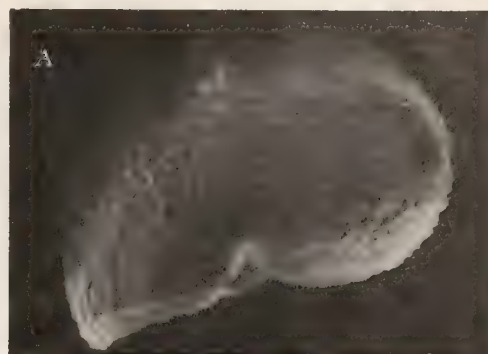


Figure 5



0.1 mm



0.1 mm

Scanning electron photomicrographs show that at hatching the veliger shell had a rough granular surface (Figure 6). *Simnia barbarensis* possessed a thickened outer shell lip and a ridge along the columellar base. *Simnia aequalis* showed neither of these sculptural characters (Figure 7). The outer lip of both species had a central tooth which separated the two sinuses supporting the velum; the tooth was more prominent in *S. aequalis* (Figure 6).

The larvae of both species developed significantly faster at 18°C than at 14°C. At both temperatures *Simnia aequalis* passed through each stage significantly faster than *Simnia barbarensis* (Table 2). *S. aequalis* hatched out of the capsules sooner than *S. barbarensis* at both temperatures; however, this difference was non-significant (Table 2). There was no difference in the survival rate of *S. aequalis* and *S. barbarensis* at 14°C and 18°C.

DISCUSSION

EGG CAPSULES

Capsule shape differs slightly in the family Ovulidae, being round in some species and oval in others. This may be due to the "smoothness" of the surface upon which they are laid (i.e., on branches of the host gorgonian). Egg capsules of *Cyphoma gibbosum* (CROVO, 1974), *Neosimnia acicularis* (ADAMS, 1968), *Neosimnia uniplicata* (PATTON, 1972), *Simnia patula* (LEBOUR, 1932), and *Simnia spelta* (THIRIOT-QUIÉVREUX, 1967) are similar to those of *Simnia aequalis* and *Simnia barbarensis*. These ovulids lay eggs in capsules joined to each other by a fibrous membrane.

Damage to the host cnidarian as a result of egg laying varies among ovulids. Branches of *Lophogorgia rigida* are not damaged by egg masses of *Simnia aequalis*, but *Simnia barbarensis* lays its capsules only after removing the flesh of its host *Acanthoptilum gracile*. Ovulids appear to require a hard surface on which to lay their egg masses, thus *Simnia barbarensis* strips its host's soft tissues and lays its egg capsules on the internal skeleton. *Neosimnia uniplicata* egg masses do not damage branches of *Leptogorgia virgulata* (PATTON, 1972), while *Simnia spelta* egg masses usually cause necrosis of the underlying tissue of its host, *Eunicella stricta* (THEODOR, 1967).

LARVAL DEVELOPMENT

Ovulids undergo "mixed development" (PECHENIK, 1979). That is, they incorporate aspects of both direct and in-

direct (pelagic) development (MILEIKOVSKI, 1971), but their development is ecologically distinct from either of these two categories. Direct development occurs within capsules as the larvae pass through 4 stages prior to hatching. Previous investigators have ignored this aspect of ovulid development, thus no comparisons are possible. Pelagic development of planktotrophic veligers begins with hatching and ends with settlement on the appropriate substrate followed by metamorphosis.

After hatching, veliger shells of *Simnia aequalis* and *Simnia barbarensis* are pinkish-brown in color. *Simnia patula*, *Simnia spelta*, and *Neosimnia acicularis* have darker shells at hatching. The shells of both *S. patula* and *N. acicularis* are purplish-brown (LEBOUR, 1932; ADAMS, 1968), while those of *S. spelta* are brownish-yellow (THIRIOT-QUIÉVREUX, 1967). The velum of *S. patula* acquires a dark border shortly after hatching. This is not present in *S. aequalis*, *S. barbarensis*, nor *S. spelta*.

Attempts to rear *Simnia aequalis* and *Simnia barbarensis* through metamorphosis were unsuccessful. Both protozoan and fungal parasites were difficult to control in spite of precautions. ADAMS (1968) however, reared *Neosimnia acicularis* through metamorphosis, and described its development and color variation. He found that *N. acicularis* had a shorter pelagic larval stage than that estimated for *Simnia patula* (LEBOUR, 1932) and *Simnia spelta* (THIRIOT-QUIÉVREUX, 1967) (30 days versus 60-90 days). Also, shell color in post-larval snails was the same as their host gorgonian regardless of the color of their parents. Color in *N. acicularis* was due to its diet, which included spicules of its gorgonian host.

Sympatric species in the family Ovulidae are often difficult to differentiate due to plasticity of shell morphology and coloration in adults. Larval descriptions of *Simnia aequalis* and *S. barbarensis* suggest characters which may be useful in differentiating them from *S. catalinensis* and *S. loebbeckeana* in Southern California and *S. avena* in the Gulf of California, respectively. Differences in veliger shell morphology between *S. aequalis* and *S. barbarensis* allow easy identification. Little information is known concerning veliger shell morphology in *S. patula*, *S. spelta*, and *Neosimnia acicularis*. However, the reticulated pattern on veliger shells of both *S. patula* and *N. acicularis* is absent in *S. aequalis*, *S. barbarensis*, and *S. spelta*. Larval descriptions from sympatric species are needed before the taxonomic usefulness of this character can be evaluated.

SUMMARY

The early development of *Simnia aequalis* and *Simnia barbarensis* is described from egg through hatching. These

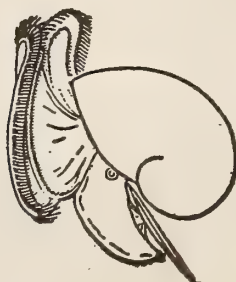
species are compared to ovulids previously described. Differences in veliger shell morphology suggest useful taxonomic characters for the family Ovulidae.

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A New Species (with Subspecies) of Fossil *Oreohelix* from New Mexico

(Gastropoda : Pulmonata : Oreohelcidae)

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(1 Plate)

INTRODUCTION

DESCRIBED HEREIN is a species, with three subspecies, of a fossil pulmonate land snail of the genus *Oreohelix*. The snails described occur in Pleistocene deposits of the Sacramento Mountains, Otero and Lincoln counties, New Mexico. This mountain range is some 100 km long, north to south, and 70 km wide, east to west. The mountains are block-faulted and tilted, with steep scarps to the west but with slopes of lower gradient to the east. The north-south trending crest of the range maintains elevations of 2775-2925 m. Forests occur generally above 2400 m elevation. Bedrock is mainly of limestones and shales of Pennsylvanian and Permian age. Pleistocene deposits are common as alluvial fill in canyons and as colluvium on hillslopes. Northward, the Sacramento Mountains merge, topographically, with the White Mountains, which comprise two major peaks, Sierra Blanca to the south and Nogal Peak to the north. The White Mountains attain higher elevations than the Sacramentos and are formed on igneous bedrock.

Localities of collections are indicated hereafter. Abbreviations used in designating repositories of types are: ANSP: The Academy of Natural Sciences of Philadelphia; DMNH: Dallas Museum of Natural History; UA: University of Arizona; USNM: National Museum of Natural History; UTEP: University of Texas at El Paso.

OREOHELICIDAE Wurtz, 1955

Oreohelix Pilsbry, 1904

Oreohelix oterana Metcalf, spec. nov.

Diagnosis: A large *Oreohelix* with relatively smooth shell, embryonic whorls with very low contour and smooth dorsally, bearing only low growth wrinkles on first 1.5 whorls and a few microspiral ridges on whorls 1.5-3.0; embryonic shell lirate ventrally; first few whorls keeled; narrow brownish bands present.

Considerable variation exists among populations of fossils. This variation has been dealt with by erecting three subspecies. These may be temporal subspecies in the sense of MAYR (1969: 43), reflecting evolutionary changes. However, some geographic variation may also occur, as discussed hereafter.

Oreohelix oterana oterana Metcalf, subspec. nov.

(Figures 1 and 2)

Description of Holotype: Shell relatively light in weight; 22.6 mm in diameter and 17.7 mm high; spire elevated, forming angle of 98° dorsally, rising 8.8 mm above terminus of upper lip; body whorl rounded peripherally and descending markedly to aperture; aperture 10.9 mm wide and 12.0 mm high with outer lip rounded,

aperture oriented at angle of 31° to vertical axis; umbilicus narrow, 3.5 mm wide, impinged upon slightly by expanding lip, contained 6.46 times in shell diameter; shell relatively loosely whorled with 5.25 whorls; sutures deeply impressed; whorls 1.5-2.7 with peripheral ridge adjacent to suture, produced by top of keel that is present on older whorls; first 1.5 whorls virtually smooth with very low, widely spaced growth lines, these becoming somewhat stronger on younger whorls, although shell is generally smooth; a faded brownish band occurs just below middle of body whorl, paralleled by a much narrower and dimmer band below and a slightly narrower band above on body whorl, this upper band continuing on, with interruptions, almost to beginning of whorl 3.

Variation: Variation in size and in some proportions of shells are indicated in Table 1. Development of the spire is especially variable. A few shells of adult *Oreohelix oterana oterana* show slight angulation of the body whorl, thus approaching the condition of *O. o. angularis*, described below. In some specimens as much as half the umbilicus is impinged upon by the lip. At maturity the lip becomes progressively thicker and callused.

Types: The type locality is Locality 10.

Holotype: USNM 809173.

Paratypes: (Topotypes) ANSP 352829, DMNH 5363, UA 19012, USNM 809172, UTEP 2242; (From other localities) UTEP 1736 (Loc. 4), 2081 (Loc. 12), 2166 (Loc. 9), 2232 (Loc. 14), 3875 (Loc. 13).

Oreohelix oterana angularis Metcalf, subspec. nov.

(Figures 3 and 4)

Description of Holotype: Shell 21.9 mm in diameter and 15.0 mm high; moderately elevated, spire sub-pyramidal in outline dorsally, forming angle of 105° and rising 8.6 mm above level of terminus of upper lip; peripheral angularity present around middle of body whorl; aperture round, 10.1 mm wide and 10.2 mm high, oriented at angle of 45° to vertical axis; outer lip widened at angularity; umbilicus narrow, deep, 3.9 mm wide; contained 5.6 times in shell diameter; shell with 5.7 whorls; sutures not notably impressed; embryonic whorls with very fine growth wrinkles, which grade to stronger but still relatively low wrinkles on younger whorls; a few ridges in central part of whorls 2.0-2.75; outer margin of whorls 1.75-4.5 bordered by shallow furrow and ridge (peripheral to

furrow and bordering suture) that represents top of (former) keel; color bands dim but discernible, the darkest (cinnamon brown) immediately below angularity on body whorl, below this on ventral surface are 5 exceedingly dim, interrupted color bands; a single dim band occurs on body whorl above angularity, continuing on to dorsal surfaces of other whorls but fading out on whorl 3.

Variation: Some shell dimensions and proportions are indicated in Table 1. A damaged specimen from Locality 5, not included in the table, has a diameter of 27.3 mm, largest specimen observed for the species. A sinistral specimen, 18.8 mm in diameter, was found at Locality 11 (Figure 4). Height and dorsal angularity of the spire vary, with some specimens having markedly lower spires than the holotype (as in Figure 4). As much as half of the umbilicus may be covered by the flaring lip. In some gerontic specimens the lip becomes heavily callused. Color bands, insofar as preserved, show much variation with interruptions and irregularities. From 1 to 7 brownish bands were observed below the angularity on the body whorl and up to 4 bands above the angularity.

Types: The type locality is Locality 5.

Holotype: USNM 809170.

Paratypes: (Topotypes) ANSP 352831, DMNH 5362, UA 19013, USNM 809171, UTEP 3426; (From other localities) UTEP 1691 (Loc. 7), 2230 (Loc. 8), 2233 (Loc. 11).

Oreohelix oterana lentiformis Metcalf subspec. nov.

(Figures 5 and 6)

Description of Holotype: Shell heavy, 21.0 mm in diameter and 13.8 mm high; spire low, broadly triangular, forming angle of 110° dorsally and rising 8.3 mm above terminus of upper lip; strongly carinate, except for last 0.25 of body whorl where keel weakens, top of (former) keel forming ridge at periphery of all except first 1.25 whorls; last 0.1 of body whorl descending slightly to aperture; aperture round, except for angularity at position of keel in outer lip, 9.5 mm wide and 9.6 mm high, forming angle of 44° with vertical axis, lip thickened; umbilicus broad, 4.9 mm wide, contained 4.29 times in shell diameter; shell with 5.5 whorls, embryonic whorls smooth, except for faint growth wrinkles, these becoming moderately strong on younger whorls; a few microspiral ridges occur in central part of whorls 1.75-2.25; a pale brown band occurs on body whorl below keel and a still paler, inter-

rupted brown band occurs on dorsal surface of whorls 2.5-4.5.

Variation: Some shell measurements and proportions are indicated in Table 1. The spire is variable in height and varies greatly in degree of dorsal angulation. The peristome of gerontic specimens is much thickened, producing a thick columellar callus. Up to one-fourth of the umbilicus may be covered by the adjacent lip. As many as 5-8 faded brownish bands were observed below the keel on the body whorl. These bands exhibit considerable fusion and interruption, tending to form an especially broad band immediately below the keel. The dorsal surface of the embryonic whorls retains a brownish color in some specimens.

Types: The type and only locality is Locality 6.

Holotype: USNM 809174.

Paratypes: ANSP 352830, DMNH 5361, UA 19014, USNM 809175, UTEP 1776.

Etymologies: The epithet *oterana* refers to Otero County, New Mexico, in which most localities of the species occur. The subspecific names *angularis* (angular) and *lentiformis* (lens-shaped) refer to salient features of shell morphology.

Differential Diagnoses of Subspecies: The three subspecies grade from rounded and high-spined (*oterana*) to angular and moderately elevated (*angularis*) to carinate and low-spined (*lentiformis*). Only the earliest whorls of *oterana* exhibit carination, whereas the keel is maintained into sub-adult shells in *angularis* and into adult shells in *lentiformis*. Thus, in regard to carination, *lentiformis* might be regarded as paedomorphic. Specimens of *lentiformis* are generally smaller than those of the other subspecies (Table 1). Perhaps *lentiformis* inhabited an environmentally marginal habitat (cold?) conducive to dwarfing and paedomorphism. Sutures are more strongly impressed in *oterana* than in the other subspecies. Except for specimens of *oterana* from Locality 4, the umbilicus becomes progressively more open in the series *oterana*.

Table 1

Diameters (in mm) and shell proportions for fossil populations of three subspecies of *Oreohelix oterana* and of *Oreohelix strigosa nogalensis*. For each value, mean and standard deviation (in parenthesis) are shown above and range below. Each sample contains 20 shells. Localities (= Loc.) are arranged north to south within each taxon.
(Apert. = Apertural; No. = Number of).

Taxon Loc. number	Diameter	Diameter/ Height	Height/ Apert. height	Apert. width/ Apert. height	Diameter/ No. whorls	Diameter/ Width of umbilicus
<i>Oreohelix oterana oterana</i>						
Loc. 4	21.3 (1.04) 19.2-23.0	1.34 (0.12) 1.21-1.52	1.56 (0.11) 1.46-1.77	0.95 (0.04) 0.87-1.03	3.93 (0.22) 3.68-4.32	4.04 (0.21) 3.62-4.40
Loc. 9	20.4 (1.07) 19.0-23.0	1.35 (0.08) 1.19-1.50	1.45 (0.06) 1.36-1.55	0.96 (0.04) 0.88-1.04	4.02 (0.20) 3.71-4.43	4.67 (0.35) 4.12-5.19
Loc. 10	20.9 (1.27) 18.6-23.2	1.33 (0.06) 1.20-1.42	1.51 (0.07) 1.39-1.66	0.95 (0.05) 0.85-1.03	4.05 (0.21) 3.71-4.56	4.83 (0.35) 4.16-5.40
Loc. 14	19.9 (1.38) 18.3-24.0	1.34 (0.09) 1.20-1.47	1.49 (0.11) 1.24-1.69	0.95 (0.06) 0.83-1.04	3.80 (0.31) 3.26-4.32	4.98 (0.48) 4.24-5.74
<i>Oreohelix oterana angularis</i>						
Loc. 5	23.0 (1.54) 20.0-25.4	1.25 (0.09) 1.12-1.44	1.55 (0.10) 1.43-1.71	0.96 (0.05) 0.88-1.05	4.08 (0.26) 3.77-4.52	4.08 (0.33) 3.58-4.89
Loc. 11	20.8 (1.46) 19.0-24.2	1.47 (0.09) 1.33-1.60	1.41 (0.10) 1.28-1.65	0.95 (0.05) 0.84-1.03	3.87 (0.19) 3.49-4.21	4.03 (0.30) 3.34-4.60
<i>Oreohelix oterana lentiformis</i>						
	19.2 (0.89) 17.5-21.3	1.73 (0.11) 1.54-1.96	1.43 (0.09) 1.26-1.59	1.07 (0.06) 1.00-1.18	3.72 (0.22) 3.39-4.07	3.87 (0.26) 3.24-4.25
<i>Oreohelix strigosa nogalensis</i>						
	18.1 (1.34) 16.1-20.6	1.59 (0.11) 1.42-1.86	1.33 (0.07) 1.19-1.48	0.95 (0.04) 0.88-1.02	3.40 (0.22) 3.04-3.79	3.75 (0.16) 3.45-4.09

angularis-lentiformis (Table 1). The pattern of color bands is similar in the three subspecies, although *lentiformis* exhibits a greater tendency towards fusion of bands on the ventral surface than do the others.

Embryonic shells have been preserved in matrix inside the parent shell in specimens from several localities and these are similar in the three subspecies. These embryonic shells show less evidence of weathering than older shells. Dorsally, the first 1.25 whorls are almost flat and bear a few, feeble growth wrinkles. A few microspiral ridges or cords (terminology of SOLEM, 1975: 17, 21) occur in the central and peripheral parts of whorls 1.5-3.0. These ridges are slightly more numerous (5-6) and stronger in *Oreohelix oterana lentiformis* than in the other two subspecies (3-4 ridges). The dorsal side of the keel is first evidenced between 1.25 and 1.75 whorls. In contrast to the sparse dorsal ornamentation, lirae are prominent on the embryonic shells, ventrally. In one embryo of *angularis* from Locality 5, 12 lirae were discernible, these being intersected at wide intervals by low growth lines.

Comparisons to Other Species: Three other species of *Oreohelix* are known from the Sacramento and White Mountains: (1) a small, discoidal species described in an accompanying paper (METCALF & CREWS, this volume); (2) *Oreohelix socorroensis* Pilsbry, 1905, known only as a fossil in the Sacramento Mountains and (3) *Oreohelix strigosa nogalensis* Pilsbry, 1939, which still inhabits the White Mountains, as at Localities 1 and 3, and has also been found as a fossil, as at Locality 2 (Figures 7 and 8).

Shells of *Oreohelix socorroensis* are smaller (generally less than 15 mm in diameter) than those of *O. oterana*, are strongly carinate, and exhibit strong lirae ventrally on all whorls.

Observations noted for *Oreohelix strigosa nogalensis* are based on fossil shells from Locality 2, which seem comparable, in their state of preservation, to shells of *O. oterana*. On shells of *O. strigosa nogalensis* there is no evidence of a keel on the earlier whorls such as that observed

in *O. oterana*. Shells of *O. s. nogalensis* are more tightly whorled than those of *O. oterana*. Embryonic shells of *O. s. nogalensis* differ from those of *O. oterana* in having many close-set growth lines on the dorsal surface (Figure 8). More than 10 such lines occur in the first whorl. These lines are intersected by numerous, close-set microspiral ridges that cover the dorsal surface of whorls 0.75-2.5 (Figure 8). Sculpturally, these shells resemble the shell of *Oreohelix strigosa strigosa* (Gould, 1846) illustrated by SOLEM (1975: fig. 12). Ventrally, embryonic shells of fossil *O. s. nogalensis* from Locality 2 show 8 or 9 major lirae and numerous microspiral ridges between the lirae. These minute ridges were not observed on embryonic shells of *O. oterana*.

DISCUSSION

Lack of knowledge of the geology of the widespread Pleistocene deposits of the Sacramento Mountains hampers attempts to relate the oreohelids discussed herein stratigraphically. Although widespread, sediments are exposed in few places and vary lithologically from valley to valley, reflecting local conditions of deposition.

Oreohelix oterana oterana occurs in what seem to be relatively ancient alluvial, reddish silts below valley-flanking terrace surfaces. The silts are of a massive nature and must represent a long period of Pleistocene deposition under rather uniform conditions. This subspecies has been found only along canyons dissecting the eastern slope of the Sacramento Mountains.

Oreohelix oterana angularis has been found in exposures mainly on the western slope of the mountains, except for its occurrence in the James Canyon drainage on the east slope (Locality 11 and elsewhere). It has been found at higher elevations than *O. o. oterana* and in some deposits of colluvial aspect, as at Locality 7.

Shells of *Oreohelix oterana lentiformis* have been found only at Locality 6 in upper Tularosa Canyon in colluvial hillslope deposits. Here it occurs with the similarly re-

Explanation of Figures 1 to 8

Figure 1: Holotype, *Oreohelix oterana oterana* Metcalf, subsp. nov.; USNM 809173; 22.6 mm diameter

Figure 2: Shell apex of *Oreohelix oterana oterana*, paratype from Locality 10 × 30

Figure 3: Holotype, *Oreohelix oterana angularis* Metcalf, subsp. nov.; USNM 809170; 21.9 mm diameter

Figure 4: Sinistral specimen of *Oreohelix oterana angularis* from Locality 11; 18.8 mm diameter

Figure 5: Holotype, *Oreohelix oterana lentiformis* Metcalf, subsp. nov.; USNM 809174; 21.0 mm diameter

Figure 6: Shell apex of *Oreohelix oterana lentiformis*, paratype from Locality 6 × 42

Figure 7: Fossil shell of *Oreohelix strigosa nogalensis* Pilsbry, 1939, from Locality 2; 17.9 mm diameter

Figure 8: Shell apex of *Oreohelix strigosa nogalensis* from Locality 2 (fossil) × 40

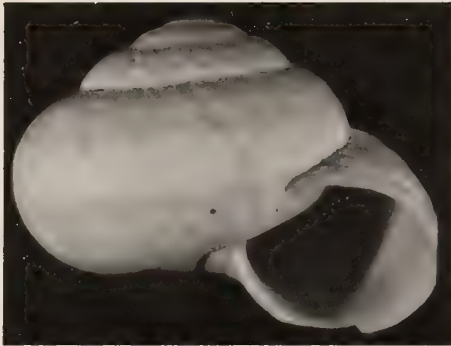


Figure 1

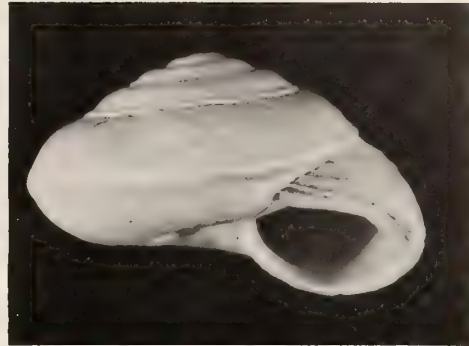


Figure 5



Figure 2



Figure 6

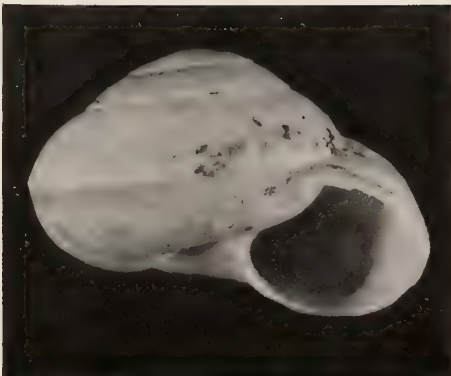


Figure 3

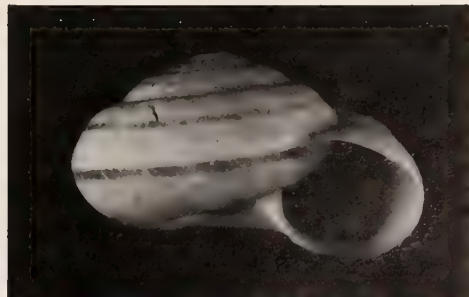


Figure 7

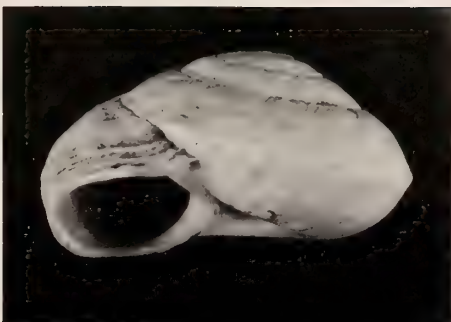


Figure 4

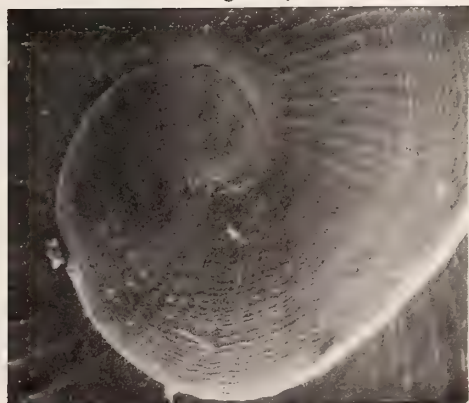


Figure 8

stricted, fossil polygyrid snail *Ashmunella tularosana* Metcalf, 1973. Failure to find these two species elsewhere suggests that deposits of this age are rarely exposed in the Sacramento Mountains.

It seems that the subspecies described are variously (and complexly) separated both stratigraphically and geographically. Localities (including several not listed herein) range from 1770 to 2290 m in elevation except for Locality 7, at 2530 m. This suggests that the species flourished best at middle, rather than highest, elevations in the mountain range. Periglacial deposits, indicating a frigid habitat during times of Pleistocene glaciations, are widespread at higher elevations in the mountains (GALLOWAY, 1970). Thus, the high crest of the range may have been a barrier to east-west gene flow during colder episodes. This and possibly other geographic isolating features, such as inter-canyon ridges, seem to have been conducive to a modest radiation in the *Oreohelix oterana* complex. Such radiations are seen elsewhere in oreohelids in mountain ranges of the Southwest. Thus, in the Black Range, to the west in New Mexico, the complex of *Oreohelix metcalfei* Cockerell, 1905, exhibits a similar radiation, comprising a number of subspecies (METCALF, 1974; PILSBRY, 1939).

Shells of *Oreohelix oterana* have not been found in deposits that seem to be of late Wisconsinan, Pleistocene age or of Holocene age. It seems to be a species that flourished and then became extinct in the Sacramento Mountains during earlier (probably pre-Wisconsinan) times in the Pleistocene. Several species of *Ashmunella* (METCALF, 1973), some of which, like *A. tularosana*, mentioned above, occur together with *Oreohelix oterana* spp. have also become extinct. *Oreohelix socorroensis*, on the other hand, occurs in late Wisconsinan and early Holocene deposits, becoming extinct in the Holocene. The inability of oreohelids to persist to the present time in the Sacramento Mountains is puzzling. Northward, in the White Mountains, *Oreohelix strigosa nogalensis* still persists but it is seemingly uncommon there. PILSBRY (1939: 442) recorded it, living, for the western slope of Nogal Peak. Two additional localities for living specimens are indicated here (Localities 1 and 3). Fossils of *O. s. nogalensis* have been taken in Pleistocene deposits along Bonito Creek (Locality 2), 35 km east of Nogal Peak. This indicates that it has suffered reduction of range, but not to the point of extinction as in *O. oterana* and *O. socorroensis*.

Taxonomic affinities of *Oreohelix oterana* are not clear. The genus *Oreohelix* is an ancient one and was likely existing in the region at the time of initial (Miocene?) uplift of the fault block that produced the Sacramento Mountains. Perhaps *O. oterana* was a member of the original fauna of the nascent mountain range.

LOCALITIES

Localities are listed north to south with 1-4 in Lincoln County and others in Otero County, New Mexico. Localities 1-3 are in the White Mountains and yielded *Oreohelix strigosa nogalensis*. Other localities are in the Sacramento Mountains. Localities for *Oreohelix* described (type locality listed first) are: *O. o. oterana* (10, 4, 9, 12, 13, 14), *O. o. angularis* (5, 7, 8, 11) and *O. o. lentiformis* (6). Type localities for some *Ashmunella* described by METCALF (1973) are: *A. ruidosana* (4), *A. tularosana* (6) and *A. jamesensis* (10). Section subdivisions for Localities 4 and 10 were miscalculated in the earlier paper. Last entry in each description indicates elevation in meters.

1. 32°29'48" N; 105°47'44" W. NW ¼, SW ¼, Sec. 7, T. 9 S, R. 11 E. E slope of Nogal Peak. 2819 m.

2. 33°27'04" N; 105°19'36" W. 0.35 km N of center, S section boundary, Sec. 12, T. 10 S, R. 16 E. Road cut, S side of U.S. Highway 380, W of Bonito Creek bridge; 0.4 km S of Emil Fritz Spring. 1676 m.

3. 33°23'53" N; 105°51'30" W. SE ¼, NW ¼, Sec. 36, T. 10 S, R. 10 E. Three Rivers Canyon on NW slope of Sierra Blanca Peak. 2210 m.

4. 33°19'47" N; 105°36'03" W. NW ¼, SE ¼, NW ¼, Sec. 29, T. 11 S, R. 14 E. South wall of Ruidoso Canyon; cut on SE side of U.S. Highway 70 in village of Ruidoso Downs. 1963 m.

5. 33°09'09" N; 105°46'33" W. NE ¼, SE ¼, Sec. 28, T. 13 S, R. 12 E. S wall of Tularosa Canyon in Mescalero; cut on S side of road that borders shopping center and park on S; immediately E of mouth of Graveyard Canyon; 0.75 km W of St. Joseph's Mission Church. 2011 m.

6. 33°04'39" N; 105°42'41" W. NE corner, SE ¼, SW ¼, SE ¼, Sec. 19, T. 14 S, R. 13 E. Tularosa Canyon; exposure in cut on E side of Tularosa Canyon road; 0.97 km S of Firman Canyon road. 2268 m.

7. 32°57'59" N; 105°45'12" W. NW ¼, SW ¼, Sec. 35, T. 15 S, R. 12 E. Cut on E side of U.S. Highway 82, 0.9 km SSE of apex of "hairpin curve" on highway. 2530 m.

8. 32°57'00" N; 105°49'24" W. SE ¼, NW ¼, Sec. 4 (over-size), T. 16 S, R. 11 E. Village of Mountain Park; S wall of Fresno Canyon; cut on S side of Haynes Canyon road, 0.15 km S of its junction with U.S. Highway 82. 2042 m.

9. 32°55'21" N; 105°34'32" W. 0.21 km S of NW corner, Sec. 13, T. 16 S, R. 13 E. N wall of James Canyon; cut on N side of U.S. Highway 82; 1.8 km SE of entrance to Burgett Greenhouse. 2230 m.

10. 32°54'30" N; 105°30'50" W. SW ¼, NW ¼, NE ¼, Sec. 21, T. 16 S, R. 14 E. N wall of James Canyon; borrow pit on N side of U.S. Highway 82, opposite New Mexico State Highway Department buildings. 2100 m.

11. 32°54'29" N; 105°30'56" W. SE $\frac{1}{4}$, NE $\frac{1}{4}$, NW $\frac{1}{4}$, Sec. 21, T. 16 S, R. 14 E. N wall of James Canyon; cut on N side of U.S. Highway 82, immediately W (across arroyo) of Locality 10. 2097 m.

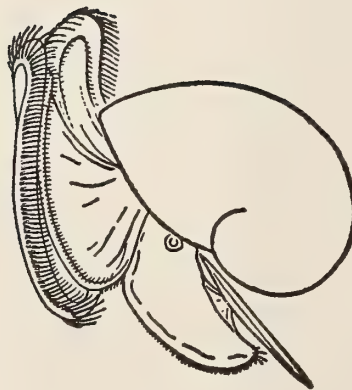
12. 32°51'28" N; 105°38'03" W. SW $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 32, T. 16 S, R. 13 E. NE wall of Cox Canyon; cut on N side of NM Highway 24, 3.9 km NW of its junction with Penasco Canyon road. 2292 m.

13. 32°50'59" N; 105°36'36" W. NW corner, Sec. 10, T. 17 S, R. 13 E. SE wall of Wills Canyon; cuts on SE side of road from Penasco Canyon to Agua Chiquita Canyon, 1.05 km WSW of its junction with Penasco Canyon road. 2240 m.

14. 32°50'57" N; 105°32'34" W. NE $\frac{1}{4}$, SE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 7, T. 17 S, R. 14 E. Cuts along Bear Canyon road, immediately below apex of "hairpin curve"; 0.22 km N of Weems Spring. 2135 m.

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A New Species of Fossil *Oreohelix*

(Pulmonata : Oreohelicidae)

from Otero County, New Mexico

BY

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(4 Text figures)

THE SPECIES OF FOSSIL PULMONATE land snail described herein has been found at a single locality in deposits of Pleistocene age, in the southeastern part of the Sacramento Mountains, Otero County, New Mexico.

OREOHELICIDAE Wurtz, 1955

Oreohelix Pilsbry, 1904

Oreohelix penascana Metcalf and Crews, spec. nov.

(Figures 1 and 2)

Diagnosis: A small, greatly depressed, carinate species, somewhat discoid in shape with ascending upper lip on body whorl of mature specimens, widely umbilicate with weakly developed growth lines dorsally and faint spiral lirae ventrally.

Description of Holotype: Shell strongly depressed; 11.6 mm in diameter and 4.0 mm in height; comprising 4.15 whorls; upper lip ascending, with body whorl, thus, expanding dorsally to height of apex; carinate peripherally, with keel at about 0.75 height of body whorl; aperture ovate horizontally, 4.9 mm wide and 3.9 mm high, oriented at 65° to vertical axis of shell; umbilicus broad and shallow, 4.2 mm wide, contained 2.76 times in diameter; suture moderately impressed, becoming deeper on younger part of body whorl; dorsal surface generally smooth with growth lines weak and irregularly spaced on earlier whorls, becoming moderate to strong on body whorl and with faint spiral lirae on body whorl; ventral surface smooth, except for low growth lines and weak spiral lirae; earliest 2.25 whorls of dorsal surface pale grayish-white, grading to pale gray mottling on whitish background by 2.75 whorls and to white on youngest part

of body whorl; ventral surface generally pale grayish-white with faded tan color band (barely discernible) below keel on body whorl.

Variation: (Based on 15 paratypes). Measurable shells range from 8.6 to 14.2 mm in diameter (mean 10.1 mm) and 3.5 to 5.4 mm in height (mean 4.1 mm). Discoidal shape and ascension of the body whorl become more marked with maturity. The peripheral keel is more strongly developed on younger whorls. Ventral lirae are fairly strongly developed in some specimens. Original coloration is poorly preserved but a few specimens show faded tan areas on the dorsal surface of the older whorls, as a band below the keel, or generally over the ventral surface.

Types: The holotype is National Museum of Natural History 784663. Paratypes include Dallas Museum of Natural History 5365 and University of Texas at El Paso 2189.

Etymology: The name *penascana* derives from Penasco Canyon, site of the type locality.

Locality: New Mexico, Otero County; Sacramento Mountains; northwest wall of Penasco Canyon, 4.8 km SSW of junction of Penasco and James canyons at Mayhill; from sediments exposed in road cut on NW side of New Mexico Highway 24/130; 32°51'06"N, 105°30'29"W; SE $\frac{1}{4}$, NE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 9, T. 17 S, R. 14 E; 2075 m elevation.

Geology: Shells occur in a rocky hillslope colluvium with matrix of pinkish silts, conformable below a heavily indurated (calichified) caprock. Deposits are unconformably overlain, to the south, by less indurated colluvium with angular stones (frost rubble) and with silty matrix of grayer color. This overlying deposit is judged to be late



Figure 1

Oreohelix penascana Metcalf & Crews, spec. nov.
Holotype; USNM 784663; side view; 11.6 mm diameter

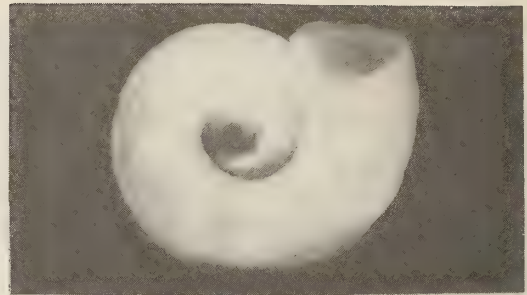


Figure 2

Oreohelix penascana Metcalf & Crews, spec. nov.
same specimen as in Figure 1; umbilical view

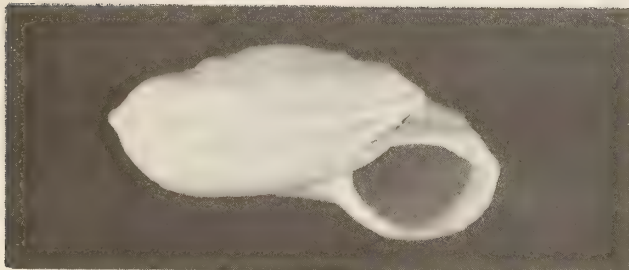


Figure 3

Oreohelix socorroensis Pilsbry, 1905
Fossil shell from Pleistocene deposits, 4.5 km NNE of Mayhill,
Otero County, New Mexico; 11.8 mm diameter; side view

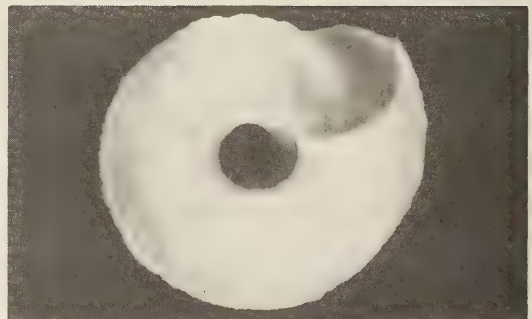


Figure 4

Oreohelix socorroensis Pilsbry, 1905
same specimen as in Figure 3; umbilical view

Wisconsinan (Pleistocene) in age and suggests that *Oreohelix penascana* occurs in sediments no younger than Early Wisconsinan in age. The development of an indurated caprock also indicates an age greater than late Wisconsinan for the sediments containing *O. penascana*.

Comparisons: *Oreohelix penascana* is probably most closely related to *Oreohelix socorroensis* Pilsbry, 1905. However, several distinctive features separate shells of the two species. The shell of *O. penascana* is more strongly depressed and discoidal in shape. Shells of *O. socorroensis*

(Figures 3 and 4) lack the ascending body whorl of *O. penascana*, have a narrower, deeper umbilicus and better developed lirae.

Oreohelix socorroensis is widespread as a fossil in the Sacramento Mountains in deposits of late Wisconsinan and early Holocene age. As noted above, it seems likely that *O. penascana* lived at an earlier time than *O. socorroensis*. The rarity of *O. penascana* may indicate that it was never of widespread occurrence or that conditions were not favorable for its preservation as a fossil or for its subsequent exposure.

Aspects of the Desiccation Tolerance of Four Species of Benthic Mollusca from Plover Cove Reservoir, Hong Kong

BY

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(1 Text figure)

INTRODUCTION

WATER LEVEL FLUCTUATIONS are a common feature of man-made lakes and may lead to the stranding of large numbers of macroinvertebrates on the exposed shores of such habitats (McLACHLAN, 1969; 1970a; KASTER & JACOBI, 1978; MARSHALL, 1978). In certain taxa, such as the Chironomidae (DIPTERA) (McLACHLAN, 1970a & b), the loss of biomass is almost immediately made up by reproduction. However, in species with a restricted breeding period any ability to survive dry conditions until the waters of the habitat return to their former levels would be of considerable selective advantage. It would be expected that freshwater taxa living in tropical climates would possess this capacity, particularly those lacking the vagility of insect populations, for the seasonal nature of precipitation in such regions enhances the likelihood of natural habitats drying out after a prolonged period without rain (*e.g.*, McLACHLAN & McLACHLAN, 1969).

Tolerance to desiccation is a capacity shared by a variety of taxa ranging from insects and molluscs (COLES, 1969a; BEADLE, 1974; STIGLINGH & VAN EEDEN, 1977) to vertebrates (*e.g.*, the lung fish *Protopterus*). Such resistance is termed aestivation and involves a reduction in metabolic rate and the production of a structure which reduces the rate of water loss, such as the "cocoon" of lung fish and the epiphragm (of mucus or calcified mucus) formed over the mouth of the shell of pulmonate gastropods (W.H.O., 1968; STIGLINGH & VAN EEDEN, 1977). A form of aestivation has been noted in certain species of ostracods which can survive in the absence of water in a "torpid" adult stage (McCLAY, 1978). The process of aestivation is dis-

tinct from cryptobiosis which involves survival during dry conditions in a state of complete dehydration (BEADLE, 1974) as seen in the drought resistant egg stages of some freshwater Microcrustacea (RZOSKA, 1961) and insect larvae (HINTON, 1960a & b) which inhabit temporary freshwater pools in tropical regions.

The following investigation is concerned with the tolerance to desiccation of four species of Mollusca found stranded on a gently sloping marginal zone of Plover Cove Reservoir, Hong Kong, after a fall in water level during 1978. It was hoped to determine whether subsequent recolonization of the marginal zone was from dormant individuals or solely as a result of animals migrating into the newly flooded habitat.

MATERIALS AND METHODS

Four species of Mollusca, *Sinotaia quadrata* (Benson, 1842) (Gastropoda: Prosobranchia: Viviparidae), *Thiara scabra* (Müller, 1774) and *Melanoides tuberculata* (Müller, 1774) (Gastropoda: Prosobranchia: Thiariidae), and *Corbicula fluminea* (Müller, 1774) (Bivalvia: Corbiculacea: Corbiculidae), were employed in the present investigation. These animals comprised the dominant elements of the benthic fauna of Plover Cove Reservoir and were collected using an Agassiz trawl operated from a boat. Test animals were maintained in aerated laboratory tanks prior to experimentation so as to ensure that only healthy specimens were used. The effect of aerial exposure in the absence of mud (which is normally present in much of the habitat of the species investigated) was tested by putting large groups of the test animals into dry enamel trays at room temperature (24°-26° C) and relative humidity

varying between 60 and 70%. Five individuals of each species were removed every day and placed in shallow dishes of water. The number of animals which had revived after 24 hours was counted and expressed as a percentage of the total removed. The experiment continued until all of the animals were killed. The effect of mud on the survival of the molluscs was investigated by placing large enamel trays containing blocks of reservoir mud into the laboratory tanks where the three species of snails were maintained. The animals were allowed to wander freely over the substrate. In the case of the bivalve, *Corbicula fluminea*, a number of individuals were put on the surface of mud blocks in enamel trays in the maintenance tanks and left undisturbed for five days, after which time they had buried themselves. All of the trays were then removed from the tanks. Gutters were cut in the mud around the margins of the trays and all of the free water was siphoned out. This was considered to represent the start of the exposure period and further procedure followed that outlined above for animals in bare trays. All test animals were washed clean of mud before the capacity for revival was determined.

The effect of size on the ability of *Corbicula fluminea* to withstand aerial desiccation in the presence and absence of mud was examined with experimental animals being divided into two groups: those less than 10 mm in length (small) and those greater than 10 mm in length (large).

RESULTS

The effects of aerial desiccation on benthic molluscs from Plover Cove Reservoir were altered according to the test species concerned and the presence or absence of reservoir mud. Survival of *Melanoides tuberculata* and *Thiara scabra* was enhanced in the presence of mud. *Thiara scabra* was more susceptible to desiccation, living for only three days in a bare dry pan, but up to two weeks in the presence of mud. In *M. tuberculata* length of survival was 8 days and 24 days, respectively, for these treatments. A similar enhancement of survival in the presence of mud was noted for *Sinotaia quadrata*, test animals surviving for 32 days in such situations as compared to 20 days in bare trays. However the effect of mud on the survival of this species was relatively less than that recorded for *M. tuberculata* or *T. scabra*, although *S. quadrata* tolerated desiccation for longer than the former species.

Although only large individuals of the three species of gastropod were used in these experiments, in the case of *Corbicula fluminea* the test animals were divided into

large and small size groups. In bare pans the smaller individuals had all died by the fourth day, while larger animals survived for 9 days. In the presence of mud the survival of both groups was enhanced, smaller animals living for 6 days and larger animals surviving until the twelfth day. These findings are summarized in Figure 1.

DISCUSSION

The inundation of a previously exposed portion of a gently sloping marginal zone of Plover Cove Reservoir, Hong Kong, produced an interesting pattern of faunal recolonization initially dominated by the gastropod *Melanoides tuberculata* (Dudgeon, in prep.). While investigations of the stranded fauna indicated that (in 1978) all of these animals had died, thereby suggesting that recolonization of the marginal zone upon inundation would be due to immigration, no information on the ability of the reservoir benthos to survive aerial exposure was available. The present study was intended to contribute to knowledge in this area.

Tolerance to desiccation was markedly altered by size. In the absence of free water, large individuals of *Corbicula fluminea* survived for approximately 30 per cent longer than smaller ones. Although the presence of mud enhanced survival in both groups, this differential was maintained. Similar size related tolerance to desiccation has been recorded in marine (COOMBS, 1973) and freshwater molluscs (HARRIS & CHARLESTON, 1977; STIGLINGH & VAN EEDEN, 1977). This phenomenon may be associated with alterations in tissue water content or shell shape during growth. However the shell shape of *C. fluminea*, whilst rather variable (HAYASHI, 1956; SINCLAIR, 1971), does not alter significantly during postembryonic development. Changes in surface to volume ratio as these animals increase in size may render larger individuals less susceptible to water loss, and due to their higher metabolic rate (DUDGEON, 1980) smaller animals would suffer from respiratory stress sooner after closing the shell valves to avoid desiccation than would larger ones; *C. fluminea* has no obvious adaptations to desiccation such as those found in the unionid bivalve *Asparthia* sp. which can aestivate for up to two years (BEADLE, 1974), or the mangrove corbiculid *Polymesoda (Geloia) erosa* which can survive out of water for over a month (Dr. B. Morton, personal communication). Indeed, the test species is comparable with *Lasmigona complanata* (Unioninae) which only survives for five days after exposure to the air (KASTER & JACOBI, 1978). A recent study of the desiccation tolerance of *C. fluminea* undertaken in North America (McMAHON, 1979) also records

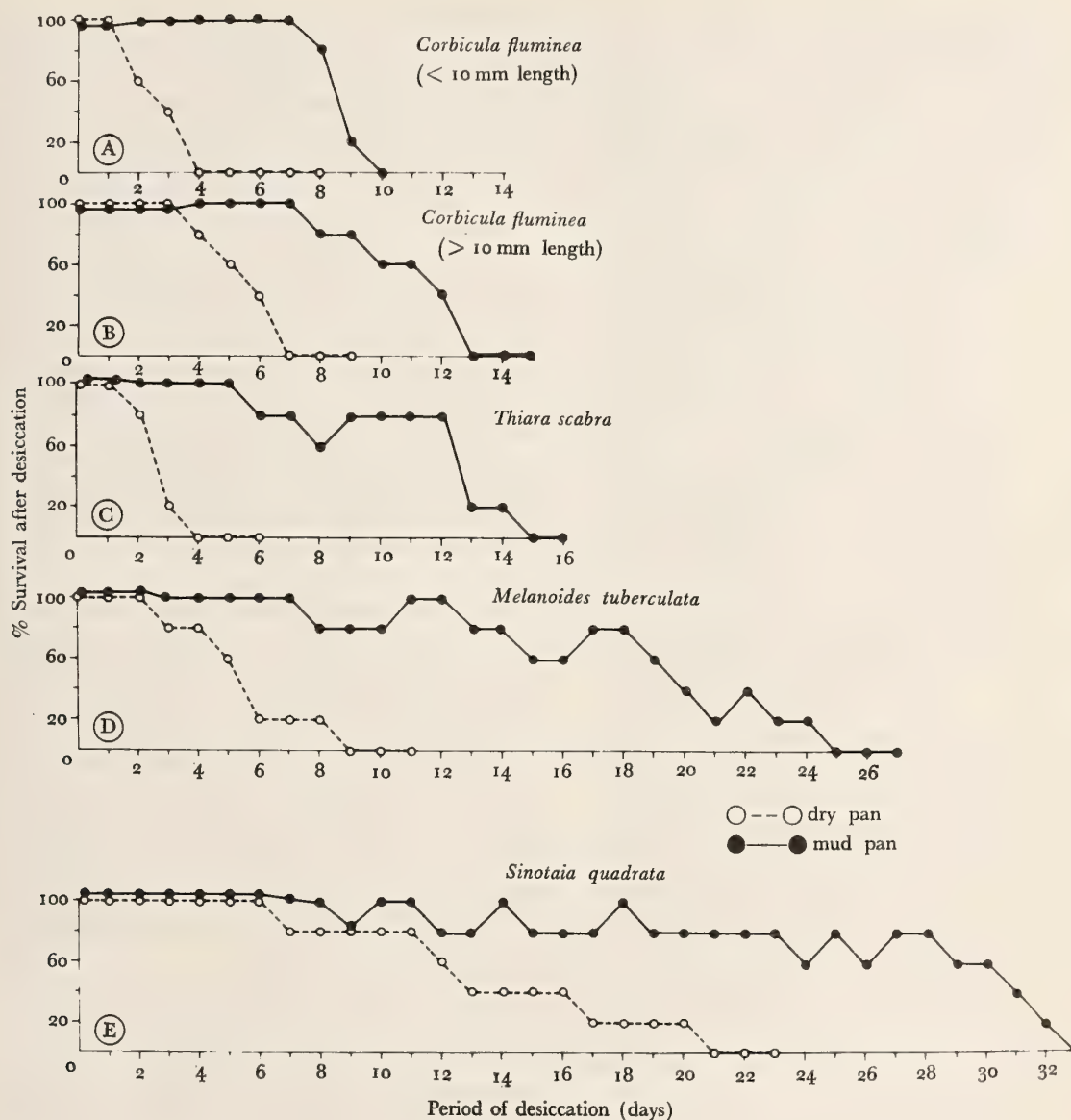


Figure 1

Graphs showing the survival of four species of Mollusca from Plover Cove Reservoir, Hong Kong, in conditions of aerial exposure in the presence or absence of mud substrate

that this species is relatively intolerant of aerial exposure, and postulates that in damp air accumulation of metabolites is the main cause of death, whilst desiccation is a more important source of fatalities in low humidities. As mud is likely to increase the relative humidity in the microhabitat immediately surrounding stranded animals, it is

possible that death in the presence of mud is due to the former cause with fatalities on the bare trays occurring as a result of desiccation. Further studies are required to elucidate these points.

Water loss through the shell is thought to be of minor significance in gastropods (CAMERON, 1970), and it is

probable that both in prosobranchs and pulmonates drying out of the peripheral tissues around the mouth of the shell occurs early in desiccation, thus slowing the rate of water loss. The response of test gastropods to the presence of mud generally resulted in the snails coming to rest with the aperture buried in the soft substrate. This greatly enhanced the survival of *Melanoides tuberculata* and *Thiara scabra* but to a much lesser degree in *Sinotaia quadrata*. Since the latter species had the longest survival time of all the species tested on bare trays, and the presence of mud, which appears to reduce water loss through the operculum of the other test snails, had a comparatively small effect on the duration of survival, it is probable that the operculum of *S. quadrata* is more impermeable to water loss than that of *T. scabra* or *M. tuberculata*. An inability to respire anaerobically for an extended period of time may thus be more important than water loss in limiting the length of time that *S. quadrata* can withstand desiccation.

The action of mud in enhancing the survival of stranded molluscs may have been due to a reduction in water loss from wholly or partially buried individuals in comparison with those animals exposed on bare trays. Aestivation of gastropods in crevices in mud is known to increase the likelihood of survival in dry conditions, as these localities have humidities which are higher and temperatures which are lower than exposed sites; hence, the rate of evaporative loss is reduced (MACHIN, 1975). Behaviour which leads to a partial or complete covering by mud can also help stranded animals to avoid lethal day-time temperatures and this was probably of particular significance on the shores of Plover Cove Reservoir where there was no shade from the direct sunlight. Indeed some gastropods are stimulated to bury in response to the onset of dry conditions, thereby increasing their chances of survival (MACHIN, *op. cit.*). Apparently, mud provides a damp microhabitat for aestivation as well as partially sealing those openings (shell valves and apertures) through which water loss can occur.

The maximum periods of survival of the species in the present investigation ranged between 9 and 31 days and they would have been unable to survive the 2½ month period of exposure of the marginal zone of Plover Cove Reservoir during early 1978. This was confirmed by observations of stranded animals in the field. Thus, in comparison to certain pulmonate gastropods such as the Planorbidae (*Biomphalaria* spp.) (W.H.O., 1968) and the Bulininae (STIGLINGH & VAN EEDEN, 1977), as well as some prosobranchs (*e.g.*, *Pila ovata*, COLES, 1969a & b), the species tested had a limited capacity for aestivation. It may be significant that those molluscs with the greatest capacity to survive periods without water are those which

inhabit temporary freshwater bodies. In fact, there appears to be a correlation between the ability to survive desiccation and the permanence of the usual habitat of the species under consideration (MACHIN, 1975). This generalization is supported by the results of the present study as *Melanoides tuberculata* and *Sinotaia quadrata*, which have relatively good tolerances of dry conditions, are frequently found in irrigation ditches, paddy fields and wet vegetable plots in Hong Kong: habitats with a restricted degree of permanence. In contrast, *Thiara scabra* is the dominant element of the macrofauna on steeply sloping rocky shores in Plover Cove Reservoir (DUDGEON, *in press*). In such situations a fall in water level exposes only a small area of the shoreline and thus reduces the chances of these snails being stranded. Similarly, *Corbicula fluminea* would not be expected to show a marked ability to survive desiccation, as its natural habitat in Hong Kong is permanently flowing streams and rivers.

The present study indicates that planned drainage and drawdowns of molluscan habitats, as has sometimes been employed as a means of controlling disease vectors (JOHN, 1970), could be a viable method of reducing the populations of a variety of pest species. *Corbicula fluminea* has become a severe nuisance in waterways in the United States (PROKOPOVITCH, 1969; McMAHON, 1977) and *Melanoides tuberculata* serves as an intermediate host of certain parasitic trematodes (MEAKINS & KAWOoya, 1973), as do some other thiarids (*e.g.*, HAMAJIMA *et al.*, 1976). On the basis of the poor capacity for survival shown by the test species in the absence of water, it would appear that drainage of the habitats of these molluscs in areas where they, or related taxa, have become pests could be a good basis for control measures.

SUMMARY

A study of the ability of four species of benthic Mollusca from Plover Cove Reservoir, Hong Kong, to withstand desiccation was undertaken. The test species were the bivalve *Corbicula fluminea* and the gastropods *Thiara scabra*, *Melanoides tuberculata* and *Sinotaia quadrata*. Large individuals of *C. fluminea* withstood aerial desiccation much better than smaller ones and allowing the animals to bury themselves in mud prior to desiccation increased survival time in this species. The presence of mud also improved the tolerance to desiccation in the three species of test gastropods. In order of increasing ability to withstand aerial exposure the experimental populations were ranked as follows: small *C. fluminea*, large *C. fluminea*, *T. scabra*, *M. tuberculata* and *S. quadrata*.

The results were discussed with reference to what is known of the biology of these species in Hong Kong and available information concerning molluscs in other regions. It is concluded that aestivating individuals of the test species would not be significant colonizers of the marginal zone of Plover Cove Reservoir when it was flooded in the summer of 1978 following a 2½ month period of aerial exposure and desiccation.

ACKNOWLEDGMENTS

This study was undertaken while I was working for a doctoral degree in the Department of Zoology, the University of Hong Kong, and I am grateful for facilities provided by that institution. I should also like to thank the Waterworks Office, Government of Hong Kong, without whose cooperation this investigation would not have been possible.

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Shape Irregularity in *Pedicularia californica*

BY

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(1 Plate)

IN A PREVIOUS PUBLICATION (SCHMIEDER, 1980), the author described specimens of *Pedicularia californica* (Newcomb, 1864) collected at Cordell Bank, W of Pt. Reyes, California, and presented evidence that *P. ovuliformis* (Berry, 1946) is a growth phase of *P. californica*, not a separate species. At that time, the cause of the irregularity in the shape of the shell was not clear. Subsequent expeditions to the Bank by the author and colleagues using scuba have yielded additional specimens and observations which explain the irregularity.

Five specimens were obtained from depths of approximately 45 m on 14 September 1980, and one from a similar depth on 10 October 1980. The locations were very near Craines Point, from which the first specimens were taken in October 1978. Refinements in positioning indicate this point to be very near Lat. $37^{\circ}58.75'$, Long. $123^{\circ}25.23'$, which differs slightly from the previous determination. Conditions of the water and substrate were similar to those in 1978.

The new specimens are very similar to those in the previous collection, and their length/width ratios fall very close to the linear relationship determined earlier (SCHMIEDER, 1980). Underwater photographs by D. Dvorak, W. Kruse, and J. Seawell show *Pedicularia* living on its *Stylantheca* substrate.

Figure 1 is a photograph of one of the specimens which was collected live on its *Stylantheca* substrate. This specimen unambiguously demonstrates the cause of the shape

irregularity: simple conformation to the substrate. The same habit was mentioned by ARNOUD & ZIBROWIUS (1979) in reference to *Pedicularia sicula*. The specimen in Figure 1 exhibits the darker core formerly named *P. ovuliformis*, plus the irregular extended outer lip of *P. californica*. This outer lip fits exactly into the branches of *Stylantheca* around the point of attachment. When the specimen was removed, a shallow scar due to retarded growth was evident, indicating an extended residence there.

Thus we conclude that *Pedicularia californica* exists in the mobile phase *P. ovuliformis*, perhaps using its extensive dentition and crenulations for grazing, eventually settling into a protective crotch in *Stylantheca* and extending its shell to conform to the branches, thereby becoming *P. californica*.

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Figure 1

Photograph of *Pedicularia californica* living on its *Stylanthea* substrate

A New Middle Jurassic Bivalve Genus, *Agrawalimya*, from Kachchh (Gujarat), India

BY

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(1 Plate; 1 Text figure)

INTRODUCTION

THE KACHCHH JURASSIC bivalve fauna is well known for its diversity and abundance. More than 35 families are known so far; many of them have been discovered only during the last decade by the members of the Banaras Hindu University team. Some families are very abundantly represented, while others are poorly represented. Pholadomyidae Gray is one of these groups. This family was initially known only by a few species of *Pholadomya* G. B. Sowerby. Later several other genera of this family were found.

The present genus has been created for an oblong, compressed and gaping bivalve with a peculiar shell surface and ornamentation found in the Bathonian-Callovian (Middle Jurassic) rocks of Pachchham Island, Kachchh district (Gujarat), India. In the type locality it occurs in strata which have yielded the Bathonian ammonites *Gracilisphinctes* Buckman, *Bullatimorphites* Buckman, and *Micromphalites* Buckman, and also in the younger beds yielding *Macrocephalites* Zittel. This genus does not agree with any of the known Jurassic bivalve genera. Unfortunately, the hinge and internal features are not exposed on any of the specimens in the present collection. It is, therefore, difficult to ascertain the true biological affinities of this taxon. However, it has some similarities in external features with *Girardotia* de Loriol, discussed later; for this reason it has been assigned to the family Pholadomyidae.

Systematic Palaeontology

CLASS	- BIVALVIA Linnaeus, 1758
SUBCLASS	- ANOMALODESMATA Dall, 1889
ORDER	- PHOLADOMYOIDA Newell, 1965
SUPERFAMILY	- PANDORACEA Rafinesque, 1815
FAMILY	- PHOLADOMYIDAE Gray, 1847
Genus	- <i>Agrawalimya</i> gen. nov.

Etymology: The genus has been named for Professor Dr. Agrawal of the Banaras Hindu University, an eminent Palaeontologist and leader of the Banaras Hindu University team investigating the Jurassic fauna of Kachchh.

Type species: *Agrawalimya pseudosulcata* spec. nov., Bathonian-Callovian, Pachchham Island, Kachchh (Gujarat), India.

Generic Diagnosis: Shell equivalve, longitudinally sub-elliptical, appreciably inequilateral, moderately inflated, and with narrow anterior and broad posterior gape; umbones compressed, angular and slightly prosogyrous; a faint sulcus with asymmetrically inclined walls extends from the mid umbo to a point just anterior to the middle of the ventral margin; shell surface anterior to the sulcus

at a higher level than that posterior to it; ornamentation consisting of concentric ribs, stronger on the anterior and posterior parts but very faint in the middle; ligament external, lunule faint; escutcheon absent.

Remarks: From the morphologic characters noted above, it is evident that the genus cannot be conveniently referred to any of the known families. Its internal features, like those of *Girardotia* de Loriol (1903: 133), are unknown, and thus do not help in a familial assignment. *Girardotia*, a genus referred to the family Pholadomyidae (in MOORE *et al.*: N827) has a comparable shell outline and few external surface features. However, the genus differs from *Agrawalimya* in having unequal valves, radial ornamentation, an uniformly curved surface and deep narrow groove with symmetrically inclined walls meeting the ventral margin posteriorly. The inequivalved nature and presence of the radial groove are characters which do not fit those of the family Pholadomyidae. However, following COX & NEWELL (in MOORE *et al.*, 1969: N832), the present authors are also referring this new genus to that family, though not very confidently.

Agrawalimya pseudosulcata Singh, Jaitly & Pandey,
spec. nov.

(Figures 1 to 3, 4)

Etymology: The specific name refers to the sulcus-like depression formed by the depressed groove on the shell surface.

Diagnosis: As for the genus.

Material: Five bivalved specimens and one left valve adhering to a shell of *Macrocephalites* (*Macrocephalites*) *formosus* (J. de C. Sowerby).

Repository: Palaeontological laboratory, Department of Geology, Banaras Hindu University, Varanasi 221005, India.

Occurrence: Bathonian – N of Sadhara (Gora Dongar) and S of Pachmai Pir (Kala Dongar); Callovian – NNW of Sadhara and S of Juna (Gora Dongar).

Description: Shell equivalve, appreciably inequilateral, moderately inflated, longitudinally subelliptical, gradually widening posteriorly and with a narrow anterior but broad posterior gape. Umbones obtusely angular, compressed, only slightly dorsal to hinge, feebly prosogyrous and situated at about the anterior third of the shell. Lunule faint and shallow, escutcheon absent. Antero-dorsal margin almost straight, meeting the strongly convex anterior margin in a broad curve; postero-dorsal margin long, gently convex, meeting the truncated posterior end in an obtuse angle, ventral margin straight to slightly convex. A pair of diagonal ridges diverge from the umbo at an angle of about 90°; the posterior one, meeting the postero-ventral end, is prominent throughout, obtusely angular and marks the region of maximum shell inflation; the anterior one is broadly rounded in the dorsal half but flattens ventrally and fades out before reaching the antero-ventral end of the shell. A sulcus-like, gradually widening radial depression, with steep anterior flank and very gently sloping posterior flank, extends from the umbo to a point just anterior to the middle of the ventral margin. This depression is bordered anteriorly by a sharp but low radial riblet in the umbonal region, which, however, fades out near the middle of the shell. The shell surface between the two diagonal ridges is almost flat but divided into two unequal parts by the radial depression; the anterior part is smaller and at higher level, and steps down almost vertically in the depression so that the part posterior to it is at a lower level (Figure 4a, b, c). Surface ornamentation of evenly and widely spaced narrow concentric ribs, which are coarse and prominent over the anterior and posterior parts but very faint, almost obliterated, in the area between the posterior diagonal ridge and the radial depression. Radially arranged fine pustules, scarcely visible by naked eye, are present on the surface between anterior third of the shell length and the posterior diagonal ridge. Ligament

Explanation of Figures 1 to 3

Agrawalimya pseudosulcata Singh, Jaitly & Pandey,
gen. nov., spec. nov.

Figure 1: Holotype (PG/98/24); Callovian – S of Juna (Gora Dongar) a – left valve, exterior; b – right valve, exterior; c – dorsal view, slightly inclined towards right valve

Figure 2: Paratype (PK/142/24); Bathonian – S of Pachmai Pir

(Kala Dongar) a – right valve, exterior ($\times 1.02$); b – left valve, dorsal view ($\times 1.02$)

Figure 3: Paratype (PG/263/7); Bathonian – E of Kharivow (Gora Dongar) a – left valve, exterior; b – dorsal view

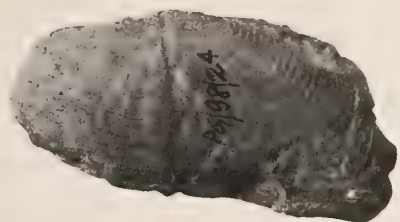


Figure 1a



Figure 1c

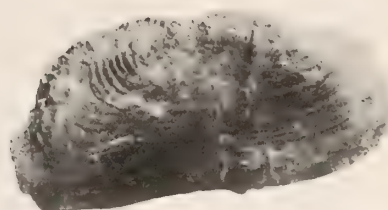


Figure 1b

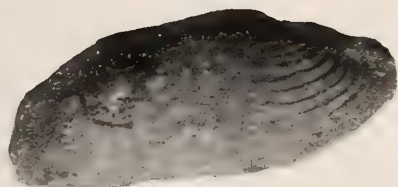


Figure 2a

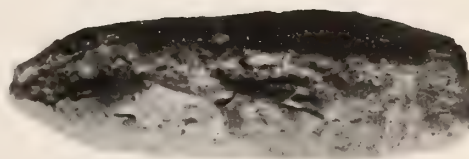


Figure 3b

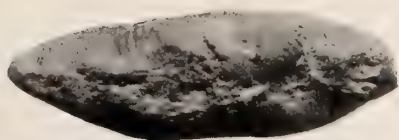


Figure 2b

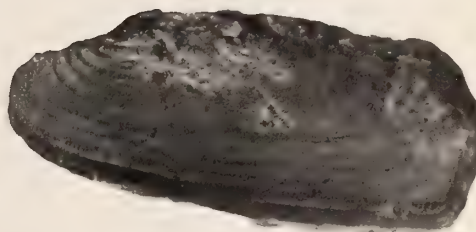


Figure 3a

external, amphidetic. Dentition and other internal characters not observable.

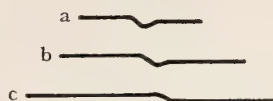


Figure 4

Diagrammatic transverse section showing the nature of the radial depression — a. in the umbonal region; — b. at the middle of the shell height; — c. near the ventral margin

Dimensions: The abbreviations used are: L — Length; H — Height; I — Inflation. The figures in parentheses represent percentage with respect to length.

Specimen No.	L	H	I
PG/98/24 (Holotype)	51.6	28.0 (54.2)	17.8 (34.4)
PG/256/12 (Paratype)	66.0	28.0 (42.4)	19.5 (29.5)
PG/263/7 (")	61.4	28.0 (45.7)	19.8 (32.2)
PK/142/24 (")	51.0	21.5 (42.1)	16.5 (32.3)
PK/142/23 (")	31.0	16.5 (53.2)	11.5 (37.1)

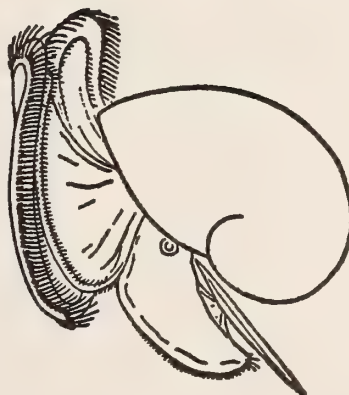
Remarks: The only taxon to which this species has any resemblance is *Girardotia elegans* DE LORIO (1903: 134, pl. 18, figs. 1a & 1b) also (in MOORE *et al.*, 1969: N832, fig. F11, 3a, b). It can, however, be readily distinguished from that species by its equivalve shell, longitudinally subelliptical outline, absence of radial ribs, presence of only a shallow radial depression bordered anteriorly by a faint rib in the umbonal region and a step-down of the surface along the depression.

ACKNOWLEDGMENTS

The authors are grateful to Prof. Dr. S. K. Agrawal for his valuable suggestions. Thanks are due to Dr. S. Kanjilal for his conducive discussions and critical review of the paper.

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Compensatory Growth and Mortality of the Hard Clam, *Mercenaria mercenaria* (Linnaeus, 1758)¹

BY

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INTRODUCTION

THE PHENOMENON OF COMPENSATORY growth in fish populations has been described by many authors including HODGSON (1929), FORD (1933), HUBBS & COOPER (1934), HILE (1941), SCOTT (1949), GERKING (1966) and RICKER (1969, 1975). Growth compensation has been defined as the tendency for smaller fish of an age-group to catch up with larger ones [SUND, (1911) in RICKER (1969)]. RICKER (1975) more formally defined the phenomenon "as a correlation between increments in size in successive years of life among fish of a given year-class" and stated that "negative correlations indicate growth compensation, because they show that smaller fish tend to catch up with larger."

This phenomenon appears to be widespread in fish species and has been attributed at least in part to variation in time of spawning, water temperature during fry period, and differences in food availability for schools of fry (SUND, 1911). GERKING (1966) in his extensive study of bluegill growth proposed a mechanism for growth compensation. He suggested that within an age class smaller fish start growth earlier than their larger companions, thereby gaining a time advantage, assuming that the growing seasons of both end at the same time.

Overcrowding in nature as in the laboratory has been reported to inhibit growth and/or lower fecundity in molluscs (CHERNIN & MICHELSON 1957a, 1957b; EISENBERG, 1966; BERRIE, 1968; MOOIJ-VOGELAAR, JAGER & VAN DER STEEN, 1970, 1973; EVERSE, 1974; PETERSON, 1978;

ELDRIDGE, EVERSE & WHETSTONE, 1979; and others). Only BERRIE (*op. cit.*) cited an example where molluscs exhibiting density-related growth inhibition experienced rapid growth when the density of snails per volumetric unit of pond was decreased by substantial collecting and heavy rainfall. Berrie's observation of rapid shell growth is unique. The lack of information concerning compensatory growth in molluscs may have been due, in part, to the difficulty in aging molluscs.

ELDRIDGE *et al.* (1979) reported that growth rate of hard clams (*Mercenaria mercenaria* (Linnaeus, 1758) was significantly reduced by increased population density. The purpose of this study was to determine if three-year old clams that had experienced significantly reduced growth due to crowding could compensate with increased growth at a lower density. A second objective was to obtain an estimate of natural mortality for clams.

MATERIALS AND METHODS

Clams (mean = 13.0 mm shell length) obtained from Coastal Zone Resources Corporation of North Carolina in May 1975 were planted in protected trays containing approximately 14 cm of natural sediment. The clams, 5 months old at planting, were grown for 3 years (May 1975-May 1978) at densities of 290, 869 and 1159 clams/m² in a subtidal and in an intertidal location 15 m apart. The intertidal site was approximately 0.3 m above mean low water while the subtidal site was approximately 0.5 m below mean low water. Details concerning tray dimensions, tray density maintenance procedures, and location of planting site near Clark Sound, South Carolina are given in ELDRIDGE *et al.* (1979).

¹ Technical contribution no. 1864 of the South Carolina Agricultural Experiment Station, Clemson University

In May 1978, 2 400 clams were selected randomly from the above 10 000 clams held for the previous 3 years in the two tidal locations at 3 population densities. Each of 12 protected trays was planted with 200 clams (stocking density of 290 clams/m²). Clams were planted according to their previous history. For example, 6 trays were planted at the intertidal site with clams that had been raised intertidally. Two trays contained clams from the previous density of 290 clams/m²; two more trays held clams that had formerly been held at 869/m²; and the remaining two trays held clams formerly cultured at a density of 1 159/m². Six trays were planted at the subtidal site with clams raised subtidally using the same protocol. Clams raised at a density of 290/m² and replanted at that density were considered controls. Shell lengths (SL, antero-posterior axis) of all clams were measured at replanting time and at succeeding 6-month intervals from May 1978 to May 1980. Clams that died during the experiment were not replaced.

The SL of clams at initial planting were determined to be normally distributed. Mean SL (May 1978) were compared with the "t" statistic to determine if initial size differences existed between individual trays. To detect compensatory growth, correlation coefficients were calculated for 6-month intervals using the variables of mean SL and change in SL of each tray.

RESULTS AND DISCUSSION

Results of "t" tests showed that clams raised at the same density were similar in mean SL between trays (replicates) and tidal locations at start of the experiment. However, the mean SL of clams formerly held at a density of 869/m² were significantly smaller ($P < 0.05$) than those at 290/m²; and clams formerly held at 1 159/m² were significantly smaller ($P < 0.05$) than both of the lower densities. These significant differences in SL among density treatments persisted throughout the experiment.

Adjustments (compensation) to reduced population densities were observed in absolute and relative growth (Table 1). Increases in mean SL between May 1978 and May 1980 were directly proportional to original densities. Shell lengths of clams formerly held at 1 159/m² and 869/m² increased approximately 10 mm and 8.5 mm during the experiment compared to only 5 mm for clams maintained at 290/m² (Table 1).

Correlation coefficients for change in SL versus mean SL were negative for each 6-month interval (Table 2). According to RICKER's (1975) definition, this population of hard clams, 3-5 years in age, exhibited compensatory growth. Also, the results of the experiment indicated that growth adjustments were influenced by reductions in population density.

Table 1

Changes in mean shell length (SL, mm) of hard clams 3-5 years old between May 1978 and May 1980.

Original Density May 1975-1978 (Age 0-3)	Replanted Density May 1978-1980 (Age 3-5)	Tidal Location	May 1978 Initial Mean SL \pm SD (Range)	May 1980 Final Mean SL \pm SD (Range)	Change in SL (% Increase)	May 1980 Survivors of 400 Replanted Clams
290 ¹	290	I ²	56.62 \pm 4.34 (43.5 - 67.9)	61.85 \pm 5.04 (46.1 - 76.2)	5.23 (9.24)	311
290	290	S ²	57.09 \pm 4.39 (36.3 - 72.2)	61.86 \pm 4.42 (47.1 - 73.2)	4.77 (8.36)	394
869	290	I	49.14 \pm 4.96 (34.4 - 62.1)	58.86 \pm 5.13 (43.7 - 72.3)	9.72 (19.78)	290
869	290	S	50.05 \pm 5.27 (31.6 - 63.9)	57.41 \pm 4.61 (38.0 - 69.7)	7.36 (14.70)	389
1,159	290	I	45.99 \pm 5.19 (29.2 - 59.7)	56.66 \pm 4.91 (44.4 - 73.4)	10.67 (23.20)	147 ³
1,159	290	S	46.23 \pm 5.35 (31.9 - 64.6)	56.31 \pm 4.53 (42.6 - 74.7)	10.08 (21.67)	380

¹ Clams/m²

² I = intertidal, S = subtidal

³ One tray with approximately 198 clams of the original 200/tray planted in May 1978 was lost in Hurricane David, September 1979.

Table 2

Correlation coefficients for change in shell length (SL) versus mean SL of hard clams 3-5 years old for six month intervals between May 1978 and May 1980.

Six month intervals	Correlation coefficients	Number of trays	Number of individuals
May-November 1978	-0.70	12	2 362
November-May 1979	-0.77	12	2 343
May-November 1979	-0.69	11 ^a	1 922
November-May 1980	-0.25	11	1 911

^aOne tray with approximately 198 clams was lost in Hurricane David, September 1979.

The ability to compensate in growth should be considered in clam culture operations. Accounts of this phenomenon in the literature for other species, as well as our own experience in raising clams, suggest that additional studies of compensatory growth need to be done before we can understand fully the interactions between age, size, and growing seasons. In addition to population density, many other environmental factors may affect compensatory growth, but not all of these may be controllable in extensive culture operations. Hence, it is more advantageous to start work on those factors that can be easily controlled to maximize production.

INSTANTANEOUS MORTALITY RATE (Z)

Hurricane David which brushed the South Carolina coast in September 1979 caused substantial mortality to intertidal clams; however, clams in subtidal trays appeared unaffected by the storm. Thus, only subtidal clams were used to calculate the instantaneous mortality rate (Z) for the experimental period (see RICKER, 1975:9 for explanation of computations). The calculated value for (Z) was 0.0144, which is equivalent to an annual mortality rate of 1.43% (RICKER, 1975:336). This estimate should be considered as underestimate because clams were protected from predators. However, for this age group, it does suggest that mortality from sources other than predation is quite low. Further research will be necessary before more accurate estimates of natural mortality can be determined for wild populations of hard clams.

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Preparation of Radulae and Penial Styles for SEM Using 0.5 N Quaternary Ammonium Hydroxide

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(1 Plate)

TISSUE SOLUBILIZERS, such as 0.5 N quaternary ammonium hydroxide in toluene, were developed to dissociate tissues and produce a homogeneous solution suitable for liquid scintillation counting. The solutions have been formulated to digest wet proteinaceous tissues such as liver, muscle, nerve, hair and cartilage.

Experimentation with Beckman BTS-450 tissue solubilizer on radular tissue has shown that neither the teeth nor the basal radular ribbon is affected but all adjacent tissues are reduced to a clear gel from which radulae and even penial styles can be easily removed. The thoroughness with which these resistant structures are cleaned is evident in the accompanying photographs (Figures 1-6).

My experience with the standard radular preparation methods of KOH, NaOH, or kitchen bleaches (Clorox, Javex) have been disappointing, particularly with formalin fixed sacoglossan material. Timing is critical or teeth may be damaged or even lost. Small sacoglossan radulae are too easily lost in the often flocculent tissue residue or in the white crusts of evaporated KOH. The involved alkylene polyamines technique of RISSO-DOMINQUEZ (1961, 1964) is unsuited to small sacoglossans, as are sonic cleaning and gross rinsings. The long teeth of the dorid *Onchidoris bilamellata* (Linnaeus, 1767) were softened by KOH and while air drying they twisted. Distortion was not evident using tissue solubilizer (Figure 1).

A simplified and extremely satisfactory method has been devised using commercially available tissue solubilizer (Beckman BTS-450). The major advantages of this solution are firstly the tissue progressively clears, amber at first, soon revealing hard structures *in situ* which are then evident throughout the remainder of the digestion process. Secondly, volume loss from the solubilizer solution is negligible and there is no annoying peripheral crust formed, even when heated to 50°C. Thirdly, time is not critical, for tissues treated for periods of 4 hours, overnight and even 3 days produced clean teeth firmly articu-

lated on intact basal ribbons. Fourthly, the type of original tissue fixative seems unimportant, as formalin, alcohol and Bouin's fixed tissues (some from 1967 collections) were digested indiscriminately. Penial styles (as described by GASCOIGNE, 1974) can also be extracted by this technique. However, unless specimens are of breeding adults with fully differentiated penial styles, that structure will also dissociate or become spongy and unsuited for further processing.

The procedure is rather simple involving a depression slide with two concavities. The headregion, buccal mass, or radular tissue may be rinsed in water to remove some of the fixative and further wet the tissue or placed directly in a concavity filled with BTS-450 and a cover slip added. Depending on amount of tissue and temperature (I use a histological slide warming plate at 45°C) the radula may be clean in 3 hours or over night. If tough strands of ligamentous tissue attached laterally to the radula seem persistent, fresh solubilizer and more time may help, but usually these strands can be teased free.

Probing with a needle will indicate when the radula is clear of tissue and then it is moved (either slid or lifted) across the slide into toluene in the second depression. This dilutes the solubilizer and actively disperses the gel and cleans the resistant material. The radula (or penial style) is then slid up onto the bridge of the slide and rinsed with 70% alcohol and twice with 95% alcohol. It will quickly air dry but can be manipulated with needles during that period into a preferred conformation for light microscopy slide mounting or SEM stub mounting. The dried specimen is prodded free from the glass surface and transferred, using a fine needle moistened by tongue-tip saliva (GASCOIGNE, 1980).

Several features evident in these SEM photographs deserve comment. JENSEN (1980) reported the teeth of *Elysia chlorotica* Gould, 1870, as having smooth edges and MARCUS (1980) also described them as smooth and pointed,

but illustrated two teeth; one with a finely serrate edge. Figures 2 and 3 demonstrate a mid ventral (not bilateral) series of backward projecting chevron lamellae. These could effectively extend the initial puncture of a *Vaucheria* sp. cell to a long slit while withdrawing the tooth. The tooth of *Alderia modesta* (Lovén, 1844) (Figure 4), which is also adapted for feeding on *Vaucheria*, is a deep thin walled spatula which is designed to extend the initial puncture by spreading the cell walls and forming an extraction tube at the same time. Based on light microscopy of penial styles, GASCOIGNE (1974) described the inner curvature of the style of *Alderia modesta* as having "about 100 spinules, each 8 μ m long, set in a narrow band along the inner curve of the shaft." Figures 5 and 6 reveal a series of imbricated scales on the inner curvature and extending half way around the shaft. This species employs random hypodermic insemination when transferring sperm. It is evident that once jabbed into the tissues of another individual, pressure directed toward the scaly inner curvature would hold the penis in place, and conversely, pressing the smooth outer curvature against the penetrated tissues would serve to slip it out of the puncture.

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Explanation of Figures 1 to 6

Figure 1: Scanning electron micrograph of transition zone from new teeth to left and worn teeth to right of radula of *Onchidoris bilamellata* (Linnaeus, 1767). The thorough cleaning action of BTS-450 is evident in the median tooth row. Collected in Minas Basin, Nova Scotia, 20 November, 1976. Bar = 100 μ m

Figure 2: Scanning electron micrograph of *Elysia chlorotica* Gould, 1870, teeth. Note midventral row of chevron lamellae. Collected in Minas Basin, Nova Scotia, 16 January, 1967. Bar = 10 μ m

Figure 3: Scanning electron micrograph of tip of center tooth in Figure 2. Bar = 10 μ m

Figure 4: Scanning electron micrograph of terminal portions of two teeth of *Alderia modesta* (Lovén, 1844). Note mid-dorsal keel on upper tooth and deep spatular nature of nearly ventral aspect of lower tooth. Collected in Minas Basin, Nova Scotia, 10 November, 1975. Bar = 10 μ m

Figure 5: Scanning electron micrograph of penial style of *Alderia modesta* (Lovén, 1844) of Figure 4. The median collar delimits the shaft on left and larger sperm ampulla on right. Bar = 100 μ m

Figure 6: Scanning electron micrograph of inner curvature of shaft of Figure 5 showing scaley surface and boundary with smooth surface of outer curvature near top of photograph. Bar = 10 μ m



Figure 1



Figure 2



Figure 3



Figure 4

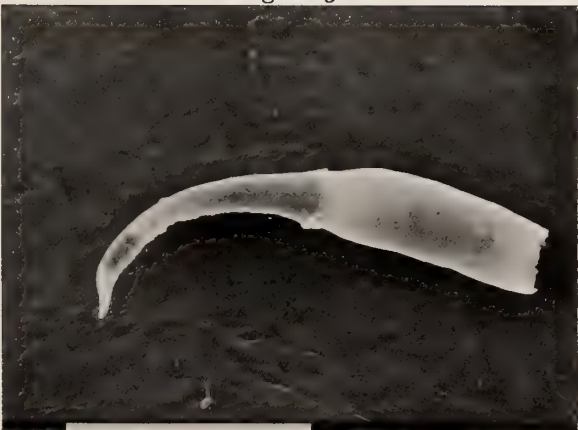


Figure 5

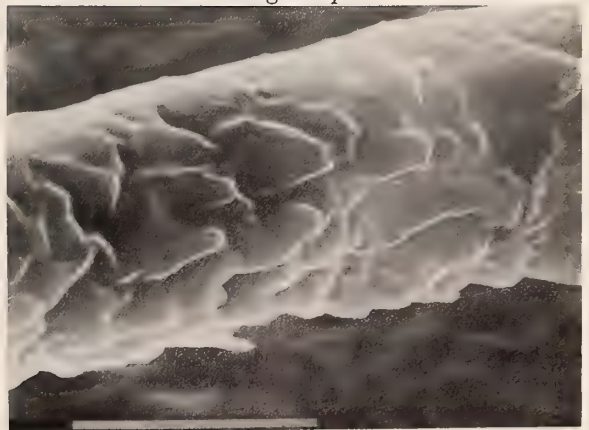


Figure 6

Population Structure of *Gemma gemma*
(Bivalvia : Veneridae)
in South San Francisco Bay, with a Comparison
to some Northeastern United States Estuarine Populations

BY

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(7 Text figures)

INTRODUCTION

Gemma gemma (Totten, 1834) (Bivalvia: Veneridae) was accidentally imported in the late 1800's to the west coast of North America with the oyster transplants from the east coast (HANNA, 1939). It has since become widely distributed (THOMPSON, 1979), and one of the most abundant organisms in San Francisco Bay, accounting for more than 35% of the biomass (wet weight) at over half of the stations it occurs (Nichols and Thompson, unpublished). Although numerous benthic survey reports list this species as a numerical dominant, no aspects of the biology or life history of West Coast populations have been described.

Gemma gemma is a small (<5.0 mm in length), ovoviviparous clam found in the subtidal and intertidal areas on the east and west coasts of North America. Studies of *G. gemma* in northeastern estuaries of the United States have shown that growth is highly seasonal, reflecting features of a temperate climate. Growth is restricted to the summer months in Massachusetts and New Jersey (GREEN & HOBSON, 1970; SELLMER, 1959), and the rate is faster in the more southern latitudes (GREEN & HOBSON, *op. cit.*) Brooding females overwinter with young conceived late in summer and release them during the following summer to avoid the harsh temperatures in fall (SELLMER, *op. cit.*).

It was presumed that *Gemma gemma* would respond quite differently to the mediterranean climate of San Francisco Bay, with its narrower temperature range and long periods of mild temperatures. The objectives of this study, therefore, were to (1) characterize the population biology of *Gemma gemma* in San Francisco Bay at

three intertidal locations, including spatial and temporal differences in density, growth, mortality and reproduction, and (2) to compare these characteristics with populations studied on the eastern coast. The major conclusions of the study are that (1) while growth was not correlated to latitude, the success and length of the reproductive season were so related, (2) the density of an upper intertidal population was controlled by competition with *Macoma balthica*, and (3) individuals are transported by water movement.

RESEARCH AREA

San Francisco Bay is a shallow, broad bay located on the Central California coast with an average depth of 6 m at mean lower low water (MLLW) or 2 m if the intertidal mudflats are included (CONOMOS, 1979). The study site is located at Sand Point in the southern end of the bay, an appendix into which no major rivers flow. The major source of freshwater in the southern bay is from exchange with water from the northern bay during maximum discharge of the Sacramento and San Joaquin Rivers (usually between December and February) (CONOMOS, *op. cit.*). A study at a nearby midwater station (from 1969 through 1976) reported a range of salinity values from 13 ppt to 33 ppt and water temperature values from 7°C to 23°C (SMITH *et al.*, 1979).

The study area consists of a broad, gently sloping intertidal mudflat with a tide range of 2.5 m. Sampling was conducted along a transect across the mudflat with a near-shore station 12 m from the edge of the marsh at 110 cm

above MLLW, a second station 28 m from the 110 cm location and 90 cm above MLLW, and the lowest station 142 m from the first, and 80 cm above MLLW. The 110 cm station is exposed at most low tides, the other two stations are exposed at 0.2 m or lower tides.

Sediment grain size was determined from replicate 17.3 cm² core samples collected bimonthly between December 1974 and November 1975 at all stations.

Coarse fractions of sediments in the upper 2 cm of each core were analyzed by the standard dry sieve method (KRUMBEIN & PETTIJOHN, 1938) and the fine fractions by the hydrophotometer method (JORDAN *et al.*, 1971). The composition of the sediment, mud with a small percentage of sand, was similar at all stations and did not differ significantly between months at any station (THOMPSON, 1979). The annual mean grain size was coarsest at the 90 cm station and the finest at the 80 cm station (Table 1).

Table 1

Annual mean grain size values
(December 1974 through November 1975)

Station	Mean phi size (Folk & Ward, 1957)	% sand	% mud
110 cm	5.99	12.94	87.06
90 cm	5.41	21.33	78.67
80 cm	6.94	11.59	88.41

Erosion and accretion of sediment were measured each month between June 1974 and January 1976, using stationary stakes placed in the mud at each station. Elevation changes, as much as 11 cm between months, were episodic, with no seasonal pattern, and changes were not consistent among stations (Figure 1).

Surface mud temperatures (2 cm deep), measured at near-monthly intervals from April 1975 through January 1976, were lowest in December 1975 at all stations (10°C) and highest in May 1975 at all stations (26°C).

MATERIALS AND METHODS

Faunal samples were collected using cores of two sizes. Three replicates were collected at monthly intervals from February 1974 through March 1975 and at near bimonthly intervals from March 1975 through January 1976 with a

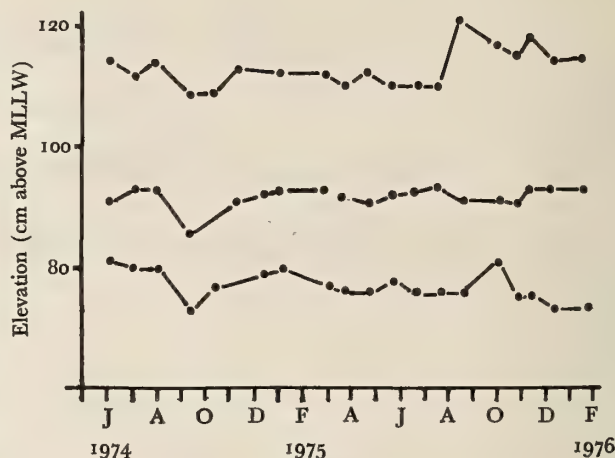


Figure 1

Elevation of the mudflat surface at the three stations

56.7 cm² corer. The cores were 20 cm deep at the 110 cm and 80 cm stations and 13 cm deep at the 90 cm station, where a shell layer made deeper cores impossible. These samples were washed through a 0.5 mm sieve, preserved in formalin for 48-72 hours, and transferred to 70% ethyl alcohol. Smaller cores (7.1 cm²) were used to collect juveniles too numerous to be counted in large core samples. Three replicates were taken with these small cores at monthly intervals from April 1974 through March 1975 at each station and preserved in 70% ethyl alcohol without sieving.

All *Gemma gemma* were measured by wet sieving in a series of graduated sieves, using a modification (THOMPSON, 1979) of the method described by GREEN & HOBSON (1970). Only animals ≥ 0.9 mm were included in the large core data during those months when small cores were available. Animals ≥ 0.7 mm, the smallest animals retained on a 0.5 mm sieve, were included in the large core data during the second year when small cores were not taken. An analysis of variance showed there to be no significant difference between the two core sizes in number of animals/size grouping in animals 0.9 to 1.4 mm long. Therefore, only animals ≤ 1.4 mm in length were included in the small core data. These data were normalized to the area of the 56.7 cm² corer and a mean was determined from the data of both cores in the overlapping region (0.9 to 1.4 mm). Unless otherwise stated, all data in this report will be based on the area of the 56.7 cm² corer and will include normalized data from small cores.

The percentage of individuals brooding at each station and the developmental state (full shell, partial shell, or

egg) of brooded juveniles were determined each month for one year, beginning in February 1974. Males were not distinguished from non-brooding females, and, therefore, brooding and non-brooding ratios include both sexes.

Ash-free dry weight (hereafter referred to as weight) was determined for animals ≥ 1.5 mm long at bimonthly intervals from June 1976 through April 1977. Brooding and non-brooding animals were weighed separately, except in June when all animals were weighed together. Animals were measured, placed in 1N HCl to remove the shell, and the tissue then ashed. Weight was regressed against the logarithm of length for each month to examine seasonal weight gain and loss.

RESULTS

Gemma gemma densities were higher throughout the study at the 80 and 90 cm stations than at the 110 cm station. Average adult *G. gemma* (individuals ≥ 0.9 mm in length) densities were 50, 300, and 250/57.6 cm² core at the 110, 90, and 80 cm stations for the two-year period. When juveniles were included, population densities were at least two times, and sometimes 20 times higher at the lower elevations than at the higher elevation. The seasonality of density fluctuations, however, was similar at all stations (Figure 2). Maximum densities occurred in July and August during the period of maximum recruitment, and minimum densities were found in the months immediately preceding recruitment (Figure 2). The population essentially disappeared in August 1975 at the 110 cm station (one animal/57.6 cm² core was found in October and December and none was found in November), when the upper intertidal mudflat was buried by 30-40 cm of decaying algae (*Polysiphonia*). The mud became anaerobic and very little benthic animal life was observed during the next few months of sampling at this station. Densities decreased in the fall of the second sampling year by as much as a factor of 10 at the deeper stations. However, this density drop could not be attributed to the decaying algae, for only small patches of algae were seen on the mudflat surface at these stations and the mud was not anaerobic.

Three cohorts (named by the year of their release, i.e., 1974 year class) were present at all stations from June 1974 through September or October 1974, when the 1972 year class was lost (Figure 3). Two cohorts remained through July 1975 at all stations. Thereafter, one cohort was present at the 80 and 90 cm locations until November 1975 when a second, very small cohort appeared at the 90 cm station. Therefore, the 1975 year class did not appear at the 80 cm station and appeared only in very

small numbers at the 90 cm station. Because juveniles were not sampled after March 1975 and would appear in the large core data only when they were ≥ 0.7 mm long,

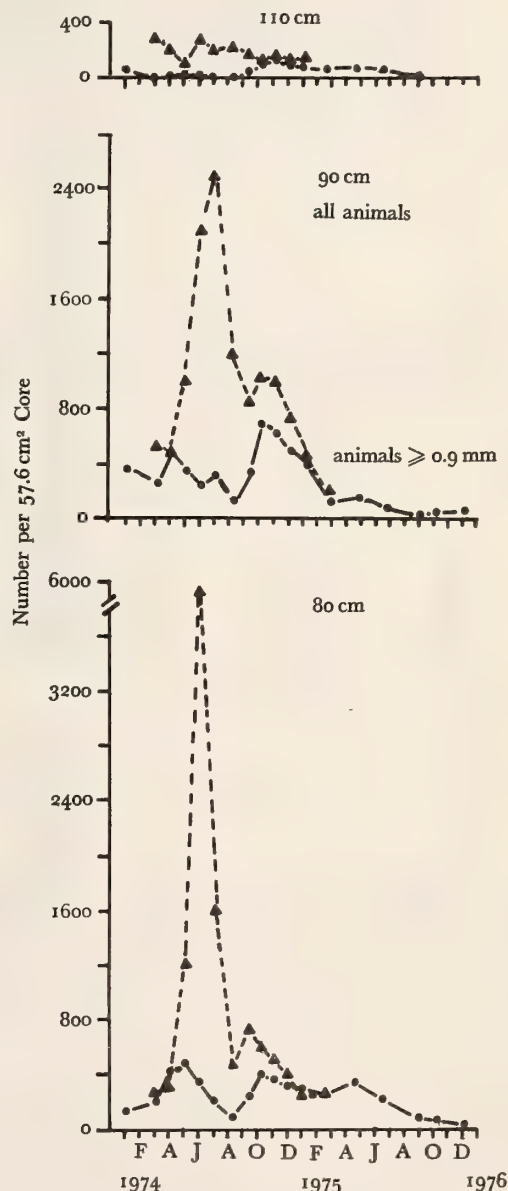


Figure 2

Densities of *Gemma gemma* at the 110, 90 and 80 cm locations. Adult (≥ 0.9 mm) densities are shown for both years; juvenile and adult data combined are shown only in the first year, as juveniles were not sampled after March 1975

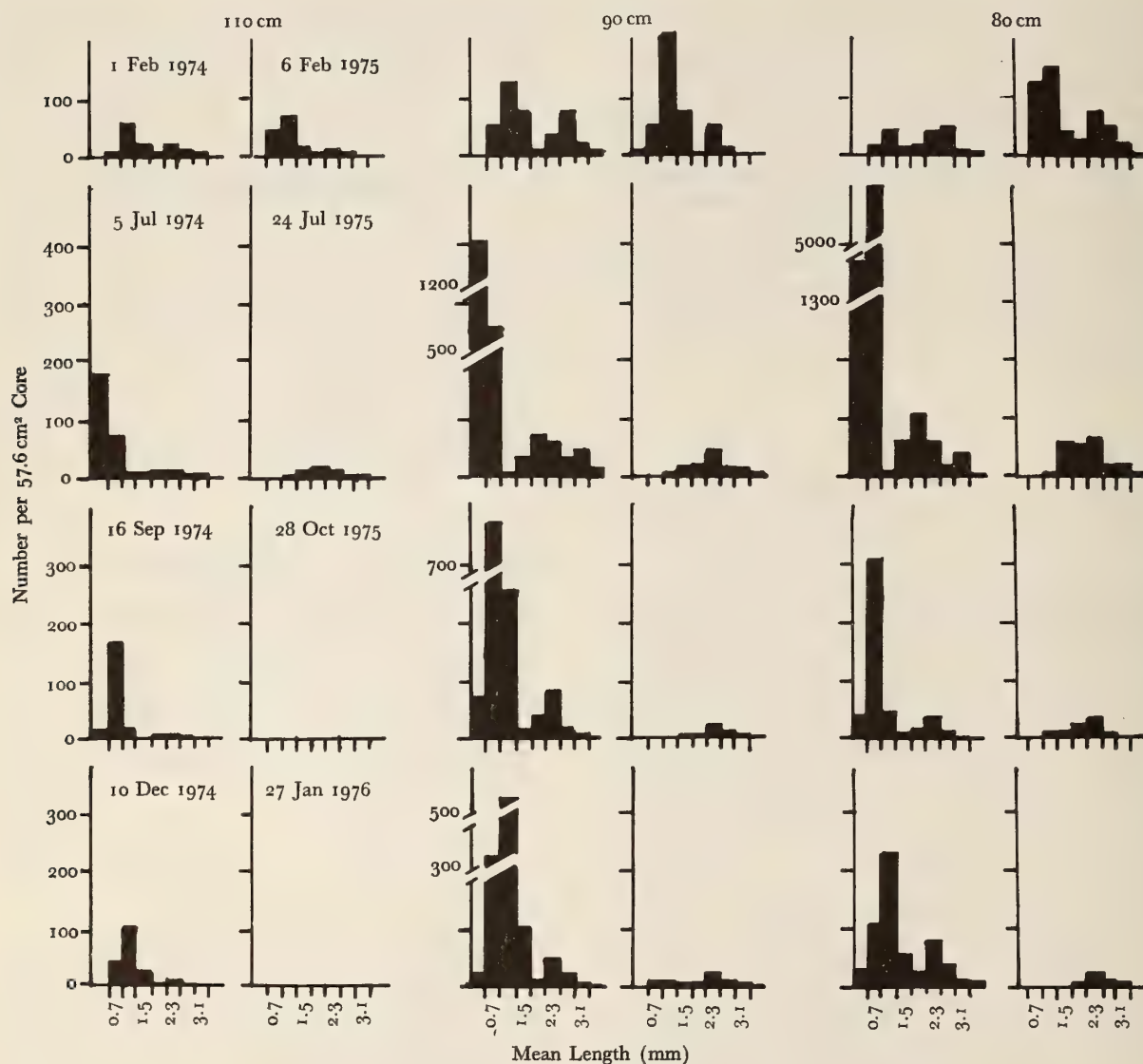


Figure 3

Size frequency distributions for *Gemma gemma* for selected months during the two years sampled. Number of animals is the mean number per 57.6 cm² core; small core counts were normalized to large core area. (Complete size frequency histograms can be seen in THOMPSON, 1979)

it is not possible to determine if the year class was released and suffered high mortality throughout the reproductive season or if it was never released. The other year classes

in 1975, the 1974 and 1973 year classes, followed a density pattern similar to that seen for individuals of the same age in 1974, the 1973 and 1972 year classes.

The degree of aggregation of adult and juvenile *Gemma gemma* was determined, using Morisita's spatial dispersion index (I_δ) (ELLIOTT, 1971) which, because of its independence of sample mean, allowed comparisons between stations, cores, and months regardless of density. Significance was tested using the chi-square test. Adult *G. gemma* (≥ 0.9 mm) were aggregated during most of the year at the two deeper stations, 12 and 11 months at the 80 and 90 cm stations, but for only 7 months at the 110 cm station (Table 2). Dispersion was not related to density, as seen

in March at the 110 cm and 90 cm stations and in May at the 80 cm station. As the number of recruits was very low from March through May, and there were no concurrent brooding adults, it is assumed these recruits came from other populations. This will be discussed later.

The length of time a female carried a brood was determined by examining the relative stage of development of brood pouches at the beginning of the reproductive season. Because eggs and partially- or fully-shelled juveniles did not occur together in the same brood, the interval

Table 2

Spatial dispersion of adult and juvenile *Gemma gemma* using Morisita's Index and Chi Square test (* $p < 0.05$, ** $p < 0.01$).

Date	110 cm		90 cm		80 cm	
	Adult I_δ	Juvenile I_δ	Adult I_δ	Juvenile I_δ	Adult I_δ	Juvenile I_δ
9 April 74	**1.10	0.98	**1.15	1.04	**1.01	
2 May 74	1.01	1.15	**1.01	1.20	**1.02	
5 June 74	*1.05	1.14	**1.02	**1.28	1.00	**1.16
5 July 74	**1.10	0.99	**1.02	**1.23	**1.10	**1.05
2 August 74	0.99	*1.07	**1.03	1.07	**1.18	**1.02
16 September 74	1.01	**1.46	**1.34	**1.05	**1.19	**1.16
14 October 74	0.99	*1.14	**1.10	**1.32	**1.07	**1.15
11 November 74	**1.03	1.43	**1.16	*1.06	**1.06	**1.14
10 December 74	1.00	0.89	**1.02	**1.10	**1.03	0.98
8 January 75	**1.06	0.75	**1.01	0.99	**1.05	1.09
6 February 75	**1.06	1.02	**1.03	1.03	**1.05	**1.42
31 March 75	*1.03	0.48	**1.02	0.60	**1.03	1.23

by the random and aggregated distribution of animals in months with equal densities (*i. e.*, December and January 1974 at the 110 cm station). Juveniles (< 0.9 mm) were aggregated at the time of release but were randomly dispersed at the beginning and end of the release period.

Generally, mortality (Figure 4) did not show any significant seasonal trends, although the mortality of the oldest year class, the 1972, increased in fall just prior to its disappearance. The expected high mortality of juveniles during the first few months was obscured by continuous recruitment.

Mature *Gemma gemma* females (≥ 1.8 mm in length, THOMPSON, 1979) began brooding in March or April 1974 at all stations and continued to do so for 6 to 10 months into early winter. The brooding season at the 110 cm station ended 3-4 months earlier and peaked 1 month later than at the deeper stations (Figure 5). Recruits appeared

between the first detection of eggs in April and the first appearance of shelled juveniles in brood pouches and of recruits in samples in June should equal the length of the brooding period. This period averaged 2 months.

Many females may brood more than once a season. Nearly 100% of adult females were brooding at the beginning of the season (Figure 5, assuming a 1:1 sex ratio as in SELLMER, 1959). Therefore, to maintain a 6-10 month reproductive season, many *Gemma gemma* must brood more than once during the year. The number of broods/female/year was determined by counting the number of adults brooding eggs each month. By assuming each brood remained in the brood pouch for 2 months before release, it was possible to calculate the percentage of mature animals beginning a new brood each month and the percentage of those carrying a brood from the previous month. The cumulative percent of animals beginning a new brood

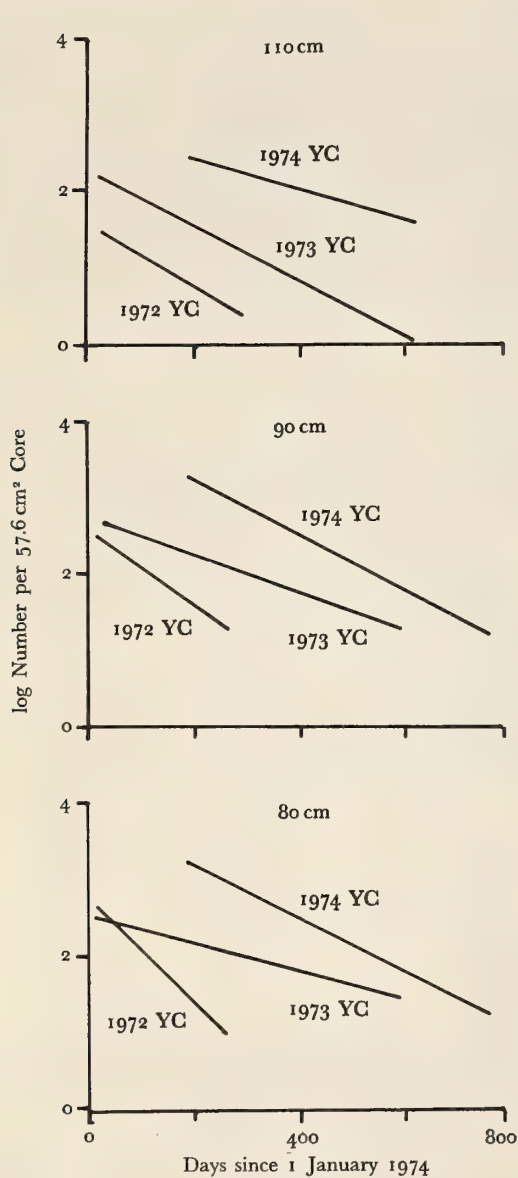


Figure 4

Mortality curves for three year classes. Only data prior to the August 1975 algae burial were used at the 110 cm station

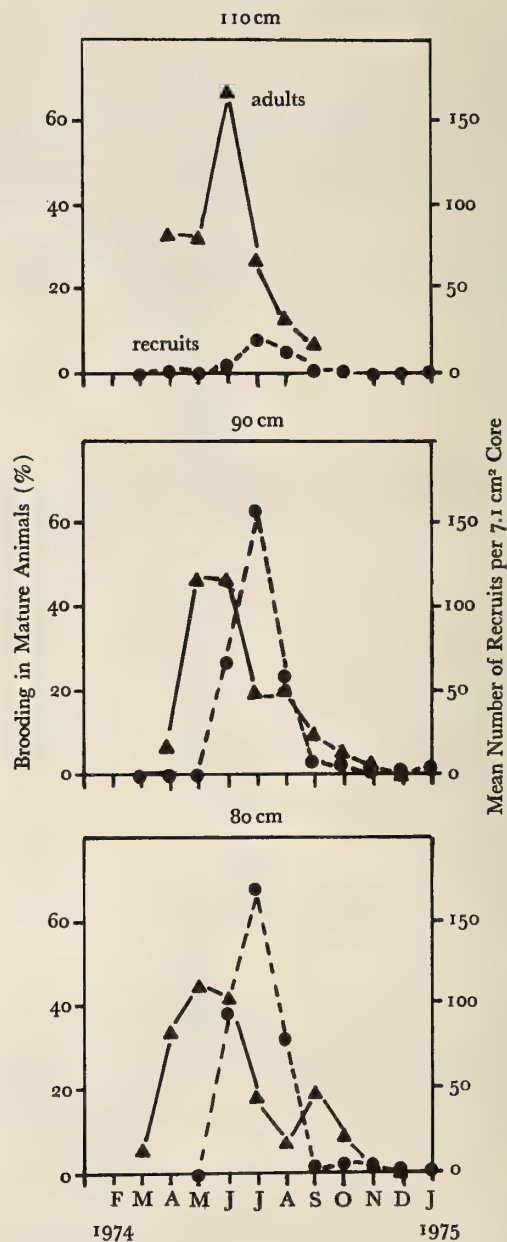


Figure 5

Percent of all mature *Gemma gemma* (male and female combined) brooding each month and the number of recruits (< 0.4 mm) per 3 cm-diameter core

during the reproductive season was then calculated. Assuming a male to female ratio of 1:1, these percentages were doubled to calculate the cumulative percent of females beginning a new brood during the year. The average number of broods per year is directly related to this percentage (Table 3).

Table 3

The relationship between the cumulative percent of new broods/year for all animals (A), the cumulative percent of new broods/year for females ($B = A \times 2$) and the number of broods/female/year ($C = B/100$).

	New broods/year all animals (cumulative %)	New broods/year females only (cumulative %)	Broods/ female/ year
Station 45	113	226	2-3
Station 46	80	160	1-2
Station 47	95	190	1-2

Growth curves for the 1973 and 1974 year classes were similar at all stations (Figure 6). Growth was fastest in spring and summer, slowed in fall, and was negligible in winter. The release of juveniles over many months resulted in a lowered mean size of the 1974 year class individuals during the first summer. However, the size frequency histograms (Figure 3) show that juveniles released in June, at about 0.3 mm, had grown to about 0.6 mm by July. Annual growth rates were the same at all stations for the 1974 year class during their first year (0.13 mm/month from June 1974 to July 1975) and for the 1973 year class during their second spring (0.11 mm/month for February 1974 to February 1975). The growth curves for the oldest year class were somewhat irregular, probably a result of the small number of animals of this size collected in their last months of life.

Weight was correlated to body length for the six sampling dates, and the resulting regression lines for non-brooding animals (Figure 7) were compared with each other by an analysis of covariance. Data were combined if slope and elevation were the same between months (*i. e.*, April-August). The slope of the lines was relatively constant throughout the year, but the elevation and thus the body weight to length ratio increased from February through December, except in June. Weight may have been overestimated in June because brooding and non-brooding

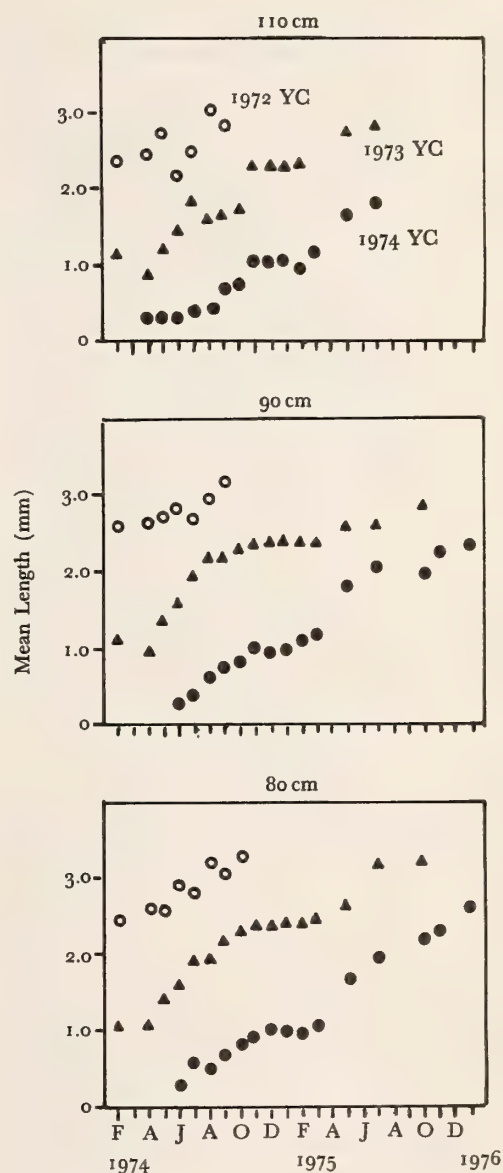


Figure 6

Mean length increase of the three year classes

animals were combined. Differences in slope generally reflected the different reproductive state of animals.

Regression lines for brooding animals, compared with those of non-brooding animals from the same month, differed only in August. The slope was the same, but an

elevation difference showed an average weight gain from a non-brooding to a brooding condition of 38%.

DISCUSSION

A comparison of population densities (Table 4) shows *Gemma gemma* to be equally, if not more successful in San Francisco Bay than in the northeastern United States. The success of *G. gemma* in San Francisco Bay may be related to the warm climate, which results in a longer reproductive period and more recruits into the population than in the northern populations. The warm climate does not, however, appear to enhance growth.

The growth study of *Gemma gemma* in San Francisco Bay was expected to augment previous studies in which a relationship between increased growth rate and higher temperatures or lower latitudes was observed (GREEN & HOBSON, 1970). Although San Francisco Bay represents the most southerly location for a *G. gemma* growth study, of the factors previously correlated to lower latitudes, increased growth period, growth rate, and maximum size and decreased life span (BACHELET, 1980; GILBERT, 1973; Nichols and Thompson, in press), only length of growth period could be correlated to the warmer climate in San Francisco Bay (Table 4). A comparison with more northern populations showed that growth rates were slower or equal, maximum size was smallest, and life span was longest in San Francisco Bay animals. Growth is initiated at

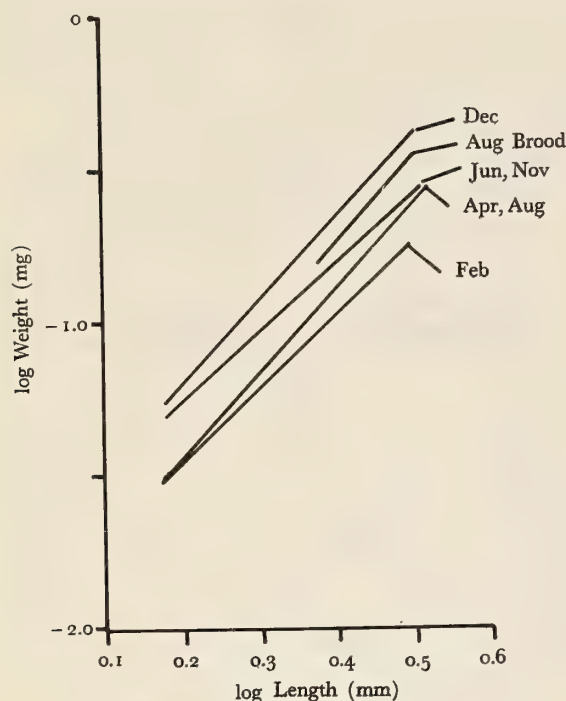


Figure 7

Relationship between weight (mg) and length (mm) for non-brooding *Gemma gemma* for one year and for brooding animals in August

Table 4

Comparison of three studies on *Gemma gemma* growth and reproduction.

	Barnstable Harbor Massachusetts (GREEN & HOBSON, 1970)	Union Beach New Jersey (SELLMER, 1959)	San Francisco Bay California
Maximum density ²	$2-3 \times 10^6/\text{m}^2$	$2 \times 10^6/\text{m}^2$	$3-4 \times 10^6/\text{m}^2$
Latitude	41° 42'	40° 27'	37° 45'
Temperature range	0-30°C (mud)	0-27.5°C (water)	7-23°C (water)
Growth period			
length	3 months	5 months	7 months
months	Jun - Aug?	Apr - Aug	Mar - Sept
Temperature range during growth	15-30°C (mud)	15-27.5° (water)	15-23°C (water)
Growth rate	0.1 mm/month	0.5 mm/month	0.1 mm/month
Maximum size	≈ 3.8 mm?	5.0 mm	3.4 mm
Lifespan	2.25 year	1.5 year	2.5 year
Fertilization period			
length	—	8-9 months	8 months
months	—	Mar - Oct or Nov	Mar - Oct
Brood release period			
length	3 months	5 months	7 months
months	June - Aug ¹	May - Sept	May - Jan
# broods/female/lifetime ³	2 - 3	1 - 2	3 - 4

¹extrapolated from figures or from generalizations in text

²highest density value if it was a unique event

³based on 2 month/brood

the same water temperature (15°C) at all locations, but it stops when temperatures drop below 15°C only in the northern populations (GREEN & HOBSON, *op. cit.*; SELLMER, 1959). Growth in San Francisco Bay animals slows in fall, prior to the drop in temperature below 15°C , indicating that some factor in addition to, or other than, temperature regulates the growth periods in these populations.

The longer reproductive period of *Gemma gemma* in San Francisco Bay, relative to northern populations, is a function of the mild fall and winter temperatures, which permit a longer brood release period. The fertilization period is the same length, but the juvenile release period increases with decreasing latitude. Broods begun late in the season (fall) are released in the early winter in San Francisco Bay, but are held by the female and released the following summer in the northern populations (GREEN & HOBSON, 1970; SELLMER, 1959). The number of successful broods per year is smaller in the northern populations, as females in their last year die before the overwintered juveniles are released (SELLMER, *op. cit.*).

The *Gemma gemma* population in this study was consistently less dense at the upper intertidal station than at the lower-elevation stations. Of the factors that control population size, competition appears to be the most likely factor, and *Macoma balthica* is the most likely competitor. *Macoma balthica*, a deposit-feeding bivalve, is significantly more dense at the 110 cm station (mean monthly density of 15 individuals/57.6 cm² core at the 110 cm station and 5 and 2/57.6 cm² core at the 90 and 80 cm stations; see NICHOLS, 1977), and has been shown to be negatively correlated with *G. gemma* population density in previous studies (GILBERT, 1969; VASSALLO, 1969). The competition between these species may be a result of the feeding activity and production of pseudofeces by *M. balthica*, which may disturb the sediment surface and make it uninhabitable for *G. gemma* (GILBERT, *op. cit.*; WOODIN, 1976). Other factors that could limit the *G. gemma* population at the 110 cm station – physiological stress due to longer and more frequent intertidal exposure, and predation – could not be demonstrated as limiting the population. The signs of physiological stress – reduced growth rate and fecundity and increased mortality rate – were not apparent at the 110 cm station relative to the other stations. Predation on *G. gemma* by shorebirds is known to occur in this mudflat (RECHER, 1966), but mortality did not measurably increase during the winter/spring migration of shorebirds, as would be expected if shorebird predation were a major factor in population control. The

other predators, bottom fish, are less likely to prey more heavily on an upper intertidal population, for they have less time to feed here than at the deeper locations.

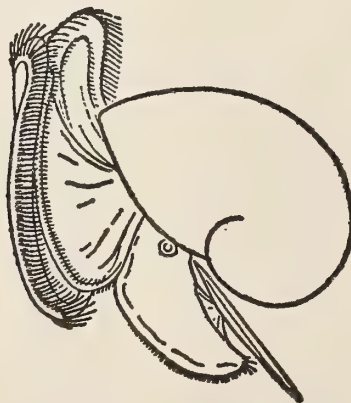
It has been assumed in most studies of *Gemma gemma* that transport of individuals by the water currents is negligible (GREEN & HOBSON, 1970; SANDERS *et al.*, 1962), or restricted to juveniles (SELLMER, 1959; SULLIVAN, 1948). The findings of this study indicate that water-borne transport may be an important factor in the dispersion of all sizes of *G. gemma*. Inconsistencies in growth and density data show that movement of *G. gemma* is episodic, primarily due to periods of increased wind, and involves different sizes of individuals at different times: 1) juvenile *G. gemma* appeared at the 110 and 90 cm stations, one to two months early relative to the reproductive state of the indigenous population. These juvenile clams were randomly distributed in contrast to the aggregation seen during most of the juvenile release period, further indicating that they were imported; 2) one-year-old individuals were imported between May and June 1974 at the 80 cm station. This was coincident with the season of increasing wind velocity and frequency in South San Francisco Bay (CONOMOS, 1979); 3) the 1974 year class density decreased and growth ceased at the 80 and 110 cm stations between July and August 1974, during a period of rapid sediment scour (Figure 1). This year class was not similarly affected at the 90 cm station, indicating that the entire year class was removed from the 80 and 110 cm stations and the animals sampled in August were recruited after the transport. The lack of transport of the 1974 year class from the 90 cm station may be due to a small, slightly elevated shell bank to the northwest of the station that may have shadowed and protected the station from strong wind waves and currents generated by the predominantly north to northwest summer winds (CONOMOS & PETERSON, 1977). Water-borne transport is no doubt responsible for the dispersal throughout the bay of *G. gemma* from the original oyster transplant sites, and the continuous maintenance of generally high densities despite periodic local declines.

ACKNOWLEDGMENTS

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NOTES & NEWS

On the Correct Spelling

of *Cadlina limbaughorum* Lance, 1962

BY

DAVID W. BEHRENS

416 Lilac Drive, Los Osos, California 93402

BEHRENS (1980: 54 and 106) introduced a new suffix, *-orum* for the trivial name, *Cadlina limbaughi* Lance, 1962. No explanation was given for the revised spelling, except that the accompanying explanation of the name derivation (p. 54) specified dual patronymy honoring Conrad and Nan Limbaugh.

Recommendation 31A (XVIth Congress of Zoology) of the International Code of Zoological Nomenclature (MAYR, 1969) states: "A species-group name, if a noun formed from a modern personal name, should usually end in . . . *-orum* if of men or of man (men) and women . . ." I was originally advised of the incorrect spelling by Mr. James R. Lance, who learned of the ICZN ruling subsequent to his publication of the species description and the patronymical recognition of the Limbaughs. Whereas LANCE (1962: 157) states "The specific name *limbaughi* was chosen to honor the late Conrad Limbaugh who was the first to collect this and many other subtidal species of opisthobranchs, and Mrs. Nan Limbaugh whose interest in this group has resulted in the acquisition of previously unknown bathymetric distributions for many forms," it seems therefore that an inadvertent error in spelling has occurred and that under Article 32a(ii) of the code (MAYR, 1969) the spelling should be changed to reflect mandatory rules. Therefore, *Cadlina limbaughorum* is a justified emendation, and is the senior objective synonym over *C. limbaughi*.

The corrected spelling, *Cadlina limbaughorum* Lance, 1962/emended Behrens, 1980/, of the name was mistakenly listed by McDONALD & NYBAKKEN (1981) as a synonym of *C. limbaughi*. Furthermore, they erroneously cite BEHRENS, 1980, as author of the species.

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Donations in Memory

of CRAWFORD NEILL CATE

Mr. CRAWFORD NEILL CATE died in San Diego after a prolonged illness. He was, for several years, a member of the Executive Board of the California Malacozoological Society where he ably represented the interests of the amateur shell collector. A number of donations to the Endowment Fund in his memory were received from: Mrs. Twila Bratcher; the Conchological Club of Southern California; Mr. and Mrs. Joseph DuShane; Miss Renée DuShane; Mrs. Ruth Greenberg; Mr. and Mrs. Wesley Heilman; Mrs. James Henry; Mrs. Slava Martin; Mrs. Elliott C. McIntire; Mr. and Mrs. R. H. Poorman; Mr. and Mrs. E. Raskin; Mrs. Marie C. Ratliff; Dr. and Mrs. Paul J. Reinsch; Mrs. F. J. Robbins; Dr. Donald R. Shasky; Mr. Gale Sphon; Mrs. Lorraine B. Toth; Mr. and Mrs. Charles Tucker; Miss M. E. Young. The Society acknowledges with gratitude these generous donations.

Another Generous Donation
from the Conchological Club
of Southern California

The CONCHOLOGICAL CLUB OF SOUTHERN CALIFORNIA has made another of its generous donations to the Veliger. Needless to say that we are very grateful for this continued

financial as well as moral support, especially in these days of economic uncertainty.

W. S. M.

The University of Redlands, Redlands, California, will be the site of the 15th Annual Meeting of the Western Society of Malacologists, June 20-23, 1982.

Symposia on the Bivalvia and the Muricidae are being planned as well as a work shop on shell photography.

New meeting facilities are being made available that should add to the comfort of those attending the scientific sessions and the displays.

For more information, please contact:

Ms. Kit Stewart
19 La Rancheria
Carmel Valley, CA 93921

Important Notice

Subscription Rates and Membership Dues

At its regular meeting on October 27, 1981, the Executive Board of the California Malacozoological Society decided, in spite of inflationary pressures, to maintain the same dues and subscription schedules as are in effect at present. This means that membership dues (which include a subscription to the *Veliger*) will remain at US\$ 18.50 plus mailing charges of US\$ 1.50 for domestic addresses and US\$ 5.00 for all foreign addresses (including Canada and Mexico). The initiation fee for new members remains at US\$ 2.00; reinstatement fee, due if membership renewals are not made to reach the Society on or before April 15 preceding the start of the new volume, will also remain at the old level of US\$ 1.00. Further, the need for a new application for membership and the payment of a new initiation fee, if membership has been permitted to lapse through non-payment of dues for 11 months after the

original deadline was reaffirmed. Similarly, the need to require the inclusion of a self-addressed, stamped envelope, if a receipt is required, was re-affirmed.

In view of the deplorable fact that the postal services throughout the world seem to become ever more expensive and also more unreliable, members are urged to lodge complaints for intolerable delays in deliveries of their journals with their local postmasters. Most likely, this will not result in better service, at least not immediately, but it may be hoped that in the long run it will lead to some improvement. Complaints to the Society cannot lead to any improvement, since we already do more than the requirements of the postal service in respect to second class mailings stipulate.

The NINE DIGIT ZIP code

is coming! And although the Postmaster General keeps asserting that its use is entirely voluntary, there are certain consequences to be anticipated if it is not used. One consequence which will affect us directly is the fact that "addressed pieces with the 9 digit code" will be entitled to a discount (this applies to bulk mailings, such as the quarterly dispatch of our journal). In other words, if the code is not used, we have to pay what really amounts to a penalty. Another consequence, which will undoubtedly apply to all mail, will be the fact that "properly coded mail" can be handled more expeditiously. The implication seems to be that those pieces that do not have the new zip code may be subject to delays in delivery.

For these reasons we earnestly ask all our subscribers and members to inform us as early as possible of their correct new zip. Since our mailing list is not on a scale as large as those of the various news weeklys, we cannot take advantage of the computer tapes that the Postal Service has prepared and will lend to the volume mailers. We will, of course, endeavor to obtain the correct codes; but we would prefer not to have to spend hours on the telephone obtaining the numbers in that way.

That the Postal Service leaves much to be desired, not only in the United States, but abroad as well, was brought home to us with the delivery of our January issue. Second class mailing requirements make it necessary for us to tie securely the various copies of a particular issue going to a particular country in a bundle with a label of the country of destination. Thus, for example, all copies going to Japan will be tied together (in the case of certain

countries we have a sufficiently large number of copies to make several bundles and combine them into a "direct sack"). Yet some individuals in each of the "direct sack"-countries received their copies from several weeks to 2 months later than others. We have, of course and unfortunately, no control over these vagaries of the postal services. Our complaints have no effect whatever.

Publication Date of THE VELIGER

THE PUBLICATION DATE of *The Veliger* is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus, our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US\$8.00 in all cases where the *Veliger* goes to domestic addresses, and a deposit of US\$25.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

We think it important to bring to the notice of all our actual and potential correspondents that the postal fee for registered articles is the highest in the world: \$3.25, regardless of destination. Further, to certain countries it is not possible to have mail pieces insured or registered. In the cases where the prospective recipient desires our communications sent as registered article, we must expect advance payment of that fee. We are unable to return manuscripts (either for reworking or with the recommendation that they be submitted elsewhere) other than by ordinary surface mail. In view of the ever more deteriorating postal services in most countries, we can obviously not assume any responsibility for the safe delivery of any

items we must dispatch. Our responsibility must and does end with our delivery to the post office of any item.

Sale of C. M. S. Publications:

Effective September 1, 1981, all back volumes still in print, both paper covered and cloth bound, will be available only from "Seashell Treasures Books," 646 30th Street, San Diego, California 92102. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. Pisor at the address given above.

Volumes 1 through 8 and 10 through 12 are out of print.

Supplements not available from "Seashell Treasures Books" are as follows:

Supplements to vol. 7 (Glossary) and 15 (Ovulidae) are sold by 'The Shell Cabinet,' P. O. Box 29, Falls Church, VI(rginia) 22046; supplement to vol. 18 (Chitons) is available from 'The Secretary,' Hopkins Marine Station, Pacific Grove, CA(lifornia) 93950.

Supplements

Supplement to Volume 3:

[Part 1: Opisthobranch Mollusks of California
by Prof. Ernst Marcus;

Part 2: The Anaspidea of California by Prof. R. Beeman, and The Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

Supplement to Volume 6: out of print.

Supplement to Volume 7: available again; see announcement elsewhere in this issue.

Supplement to Volume 11:

[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]

Supplement to Volume 14:

[The Northwest American Tellinidae by Dr. E. V. Coan]

Supplement to Volume 16:

[The Panamic-Galapagan Epitoniidae by Mrs. Helen DuShane]

[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]

Supplement to Volume 17: Our stock of this supplement is exhausted. Copies may be obtained by applying to Dr. E. C. Haderlie, U. S. Naval Post-Graduate School, Monterey, CA(lifornia) 93940.

WE ARE PLEASED to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print

editions of the publications of the Society. The microfiches are available as negative films (printed matter appearing white on black background), 105 mm × 148 mm and can be supplied immediately. The following is a list of items now ready:

Volume 1 through Volume 6: \$9.00 each.

Volume 7 through Volume 12: \$12.00 each.

Supplement to Volume 6: \$3.00; to Volume 18: \$6.00
California residents please add the appropriate amount for sales tax to the prices indicated.

Please, send your order, with check payable to Opisthobranch Newsletter, to Mr. Steven J. Long, 359 Roycroft Avenue, Long Beach, California 90814.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from "Seashell Treasures Books," 646 30th Street, San Diego, CA 92102. Orders should be sent directly there.

Single Copies of "The Veliger":

We have on hand some individual copies of earlier issues of our journal and are preparing a list of the various issues available with the prices. Some issues are present in only one or two copies, while others may be present in 10 or more copies. As we are anxious to make room, we will offer these numbers at an exceptionally low price. This list may be obtained by sending a self-addressed, stamped envelope to the Veliger, 1584 Milvia Street, Berkeley, CA (California) 94709. Foreign correspondents should enclose one international postal reply coupon. Requests for the list, for which return postage is not provided, will be ignored.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15 but before March 15 of the following year, there will be a re-instatement fee of \$1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of

the remittance. The same policy applies to new members. THE VELIGER is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of \$1.- to a percentage of the value of the draft, going as high as 33%. Therefore, we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of First Interstate Bank (formerly United California Bank). This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable, except as indicated elsewhere in this section.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of \$4.25 (to reimburse us for the expenses involved in redeeming them) and at \$0.95 per \$1.- face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Moving?

If your address is changed it will be important to notify us of the new address at least six weeks before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense.

The following charges must be made:

change of address — \$1.-

change of address and re-mailing of a returned issue

— \$2.75 minimum, but not more than actual cost to us.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

At present we are charged a minimum fee of \$15.00 on each order for new addressograph plates. For this reason we hold off on our order until 6 weeks before mailing time, the very last moment possible. If, for any reason, a member or subscriber is unable to notify us in time and also is unable to make the proper arrangement with the Post Office for forwarding our journal, we will accept a notice of change of address, accompanied by the proper fee and a typed new address on a gummed label as late as 10 days before mailing time. We regret that we are absolutely unable to accept orders for changes of address on any other basis. In view of the probable further curtailment in the services provided by the Postal Service, we expect that before long we may have to increase these time intervals.

Policy Regarding Reprints

It seems necessary to bring the following points to the notice of prospective authors:

All manuscripts submitted for inclusion in *The Veliger* are subject to review by at least two scientists; acceptance is entirely on the basis of merit of the manuscript. Although many scientific journals assess page charges, the Executive Board of our Society, for the time being at least, wishes to avoid this possible financial handicap to the younger contributors. However, because of the high cost of halftone plates, a suitable contribution to reimburse the Society must be sought.

Similarly, while it was hoped at the "birth" of *The Veliger*, that a modest number of reprints could be supplied to authors free of charge, this has not as yet become possible. We supply reprints at cost. Unfortunately, in recent years it has become "fashionable" for some authors and some institutions to ignore paying for reprints ordered and supplied in good faith or to delay payment for a year or more. This causes financial losses to the Society since our debts are paid promptly. Since the Society is in fact not making any profit, it is necessary to introduce

a policy which, it is hoped, will protect us against negligence or possible dishonesty. In the case of manuscripts from sources outside of the United States, if a manuscript is accepted, we will inform the author of the estimated cost of reprints and require a deposit in U. S. funds to cover these costs. If such a deposit is not made, we will not supply any reprints. In the case of non-payment by domestic authors or institutions, we will pursue legal recourses.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to the *Veliger* make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time; that is, 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed \$400.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, \$400.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manu-

script, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U. S. A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are submitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript — including figure explanations and the "Literature Cited" section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the "dead letter" office; in other words, it is destroyed.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

General Notice

Because of an increasing number of strange occurrences your editor deems it important to clarify our policy with respect to correspondence.

1. We never reply to letters that do not reach us. Since the U. S. postal service no longer forwards mail pieces that are not franked properly, correspondents waiting for our reply might consider the possibility that their letter falls into this category.
2. We do not acknowledge the receipt of a manuscript unless a self-addressed, stamped envelope is enclosed.
3. We do not reply to complaints regarding the non-arrival of our journal, if these complaints are made at a time when the claimed issue could not possibly have reached its destination. In view of the poor postal service throughout the world, it is unrealistic to expect, for example, the July issue in a shorter period than from 2 to 3 weeks in the United States, in less than 4 to 6 weeks in Europe, and in less than 2 to 4 months in other areas of the world; South American countries, in particular, have to expect maximum delays. It should be obvious that we are not responsible for the postal service.
4. We particularly object to complaints about non-receipt of issues which are scheduled to be published as much as 6 months after the complaint was sent! A little consideration of what is possible and what is absurd should help to obviate such untimely complaints.
5. We are receiving an increasing number of requests for our list of individual back numbers that are still available, as well as for our suggestions to prospective authors. These requests state that a self-addressed stamped envelope is enclosed — but somehow the writer must have forgotten to do so. These requests also are not answered by us.

We consider that our policy is justified for several reasons: the requirement for self-addressed, stamped envelopes has been stated in every issue of the Veliger for the past several years. Since we are a non-profit organization, we prefer to reserve our energy and our resources for productive purposes. However, we do conscientiously, and usually exhaustively, reply to all correspondence that we consider legitimate. Moreover, such correspondence is usually answered the same day as received, with the reply posted the next morning at the main post office in Berkeley. What happens afterwards is beyond our control.

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in **THE VELIGER** is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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Note: The various taxa above species are indicated by the use of different type styles as shown by the following examples, and by increasing indentation.

ORDER, Suborder, DIVISION, Subdivision, SECTION,
 SUPERFAMILY, FAMILY, Subfamily, Genus, (Subgenus)
New Taxa

Simulating Molluscan Shell Pigment Lines and States: Implications for Pattern Diversity

BY

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Department of Zoology, University of Georgia, Athens, Georgia 30602

(1 Plate)

INTRODUCTION

IT WOULD BE EASIER to understand the tremendous variety of molluscan shell pigment patterns if a common cellular basis for it were known. Several analyses (WRIGLEY, 1948; WADDINGTON & COWE, 1969; and SEILACHER, 1972) suggest that the same mechanism controls the patterns in various species. How different patterns might develop from common cellular states within a species can be seen in the evidence (LINDSAY, MS) that the divaricate pigment patterns of *Lioconcha castrensis* (Linnaeus, 1758) (Bivalvia: Veneridae) develop from different sequences of eight standard pigmentation states in the mantle.

Divaricate pigment patterns are lineages of units in which pairs of lines or edges diverge over the surface of the valve. LINDSAY (MS) presented evidence that *Lioconcha castrensis* assembles four major kinds of pattern, each from a characteristic unit made of radial and divergent lines (Figure 1). These lines, in turn, were interpreted (LINDSAY, MS) to represent different on-off combinations of three properties: 1) ability of pigmentation zones (EMBERTON, 1963) to deposit pigment; 2) to move tangentially in the margin of the mantle; and 3) the actual direction of movement. Switching movement off, for example, converts a divergent line to radial, and turning pigment deposition off ends either line. This subunitary approach makes it evident that pattern variation may depend on standard binary pigment states and transitions controlled at several cellular levels in the mantle edge.

The present report demonstrates by computer simulation, that these states and pigment lines can also account for interspecific differences among *Lioconcha castrensis* and two species of gastropod, *Oliva porphyria* (Linnaeus, 1758) and *Conus marmoreus* Linnaeus, 1758. These simulations suggest that the regulatory states which deposit radial and divergent lines may be versatile agents of shell

pigment pattern variation across a broad phylogenetic range of molluscs.

METHODS

Specimens of *Lioconcha castrensis* were kindly loaned by R. T. Abbott, Delaware Museum of Natural History; K. R. Boss, Museum of Comparative Zoology; G. M. Davis, Academy of Natural Sciences of Philadelphia (ANSP) and J. Rosewater, National Museum of Natural History (NMNH). Others are from the author's collection (DTL).

Shell pigment patterns were simulated with a program named Shelpat, written in Fortran 4 for the Control Data Corporation Cyber 74 computer at the University of Georgia. Shelpat simulates appositional growth of patterns by printing vertical and diagonal lines row by row down the computer page. Shelpat scans each row for lines. When it encounters one, it identifies the line as vertical or diagonal and decides with a random number generator whether the line continues growing, stops, or in the case of diagonals, branches.

Shelpat approaches pattern variation parsimoniously. It attempts to infer from patterns the minimum controls necessary to produce acceptable simulations of as many different patterns as possible. The program generates variation from four sets of standard control variables, rather than using new variables for each species. Each set represents a standard regulation that inspection of shell patterns and simulations has shown to be necessary for patterns to develop. The modeler simulates intra- and interspecific variation among these regulations by assigning different values to the variables.

Shelpat's control variables are based on observations (LINDSAY, MS) from *Lioconcha castrensis* that new diver-

gent lines branch from old ones, that radials begin on divergent lines, and that lines may grow, branch, or terminate (see Figure 1). The first set of variables contains probabilities that govern the fate of diagonal lines. Shelpat compares these values to uniformly distributed random numbers and prints long terminal lines, short branching ones or others depending on the choice of values. The second set controls the length of vertical lines by specifying the mean and variance of a normal distribution curve. Large values give long variable verticals, small values short uniform lines.

The third variable concerns simultaneous termination of neighboring radial lines in triangles. When given the value "on," this variable causes a terminal vertical line to end neighboring lines and when "off," terminating diagonals end neighboring radials instead. The difference allows Shelpat to print right triangles and isosceles triangles. The last set of variables decides whether converging lines terminate or branch. It contains probabilities for these events which Shelpat compares with uniform random numbers.

RESULTS

Different combinations of all four variables produce patterns that resemble those of *Lioconcha castrensis*, *Oliva porphyria*, or *Conus marmoreus*. A portion of printout corresponding to two tents from an open pattern in *L. castrensis* appears in Figure 2a. Control values were selected for relatively short diagonal lines which terminate and branch with the same frequency. Short, relatively uniform vertical lines simulate the irregular inner edges of these tents, except where divergent lines terminate neighboring verticals. The third value was "off" and the fourth, though not effective in this example, favored ter-

mination of convergent lines.

Figure 2b simulates isosceles triangles from a closed pattern to *Lioconcha*. All control variables retained the same values, except that the length of vertical lines was increased to fill the triangles.

Simulations of halved patterns from *Lioconcha* appear in Figure 2c. Here, the control values produced a long diagonal line by suppressing branching and termination. The mean and variance gave intermediate lengths to vertical lines and the third variable was turned "on" to terminate them. As a result, the first vertical line to terminate under the normal curve stops its neighbors and forms a right triangle. The next vertical to end under the curve produces the second triangle, and so on. (The mean and variance also control the number of neighbors terminated.) Though irrelevant in this example, variable four still favored termination of converging lines.

Figure 2d represents a simulation of a brush from a wide pattern in *Lioconcha*. Branching and termination were suppressed again in the diagonal lines, and the mean and variance have been increased for verticals. Simultaneous termination of verticals has been turned "off" and convergence is the same as before. Consequently, Shelpat prints a long diagonal line from which radials extend for normally distributed distances.

Other combinations of control values cause Shelpat to simulate *Oliva porphyria* and *Conus marmoreus*. *Oliva porphyria* displays patterns of divergent lines which branch from each other and end when they intersect (Figure 3b). Radial lines are reduced or absent. Shelpat produces such patterns (Figure 3b) when the control variables favor long, branching diagonal lines which terminate at intersections, and when the mean and variance for vertical lines are zero. Simultaneous termination of verticals is irrelevant under these conditions. *Conus marmoreus* requires nearly opposite values (Figure 3a). In this case, very long diagonal

Explanation of Figures 1 to 3

Figure 1: Pattern and subunits from *Lioconcha castrensis*. Patterns on the valves at the top of the figure consist of radial and divergent lines organized into the subunits at the bottom. (A) Open patterns (NMNH 247597) consist of tents; (B) closed (ANSP 254601), isosceles triangles; (C) halved patterns (ANSP 206389A), right triangles; and (D) wide patterns (ANSP 53475A), brushes. The units differ according to the number of divergent lines, the length of radial lines, and whether the radials end simultaneously. Evidence for this subunitary basis is given in Lindsay, MS. Arrows identify parts of patterns simulated by computer in Figure 2.

Bar = 1 cm

Figure 2: Simulations of *Lioconcha* shell pigment patterns.

Bar = 1 cm

The bar does not apply to simulations, which were printed at 8 lines per inch. (A) A pair of tents from a simulation of open patterns and comparable pattern from NMNH 247597. See Figure 1 for the whole valve of this and other specimens. (B) A string of isosceles triangles from a simulation of closed patterns and a sequence from ANSP 254601. (C) Right triangles simulating halved patterns and a similar sequence from ANSP 206389A. (D) A brush and similar sequence from wide patterns in ANSP 53475A. Figure 3: Simulations of patterns in *Conus* and *Oliva*. Bar = 1 cm. (A) *Conus marmoreus* (inset) and printout. DTL (unknown provenance). (B) *Oliva porphyria* (inset) and printout. DTL (unknown provenance)

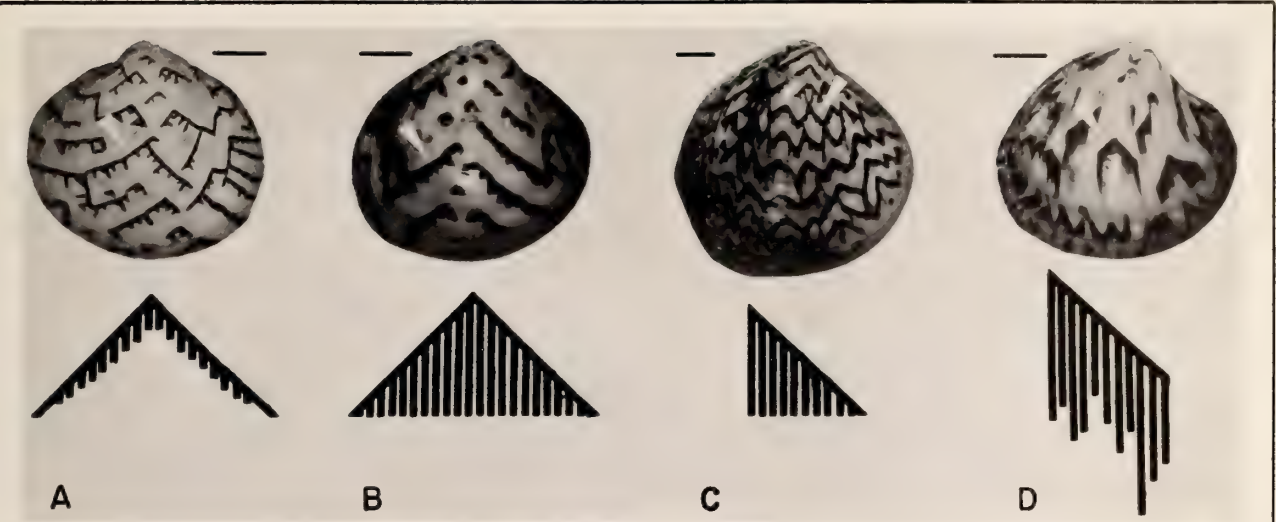


Figure 1

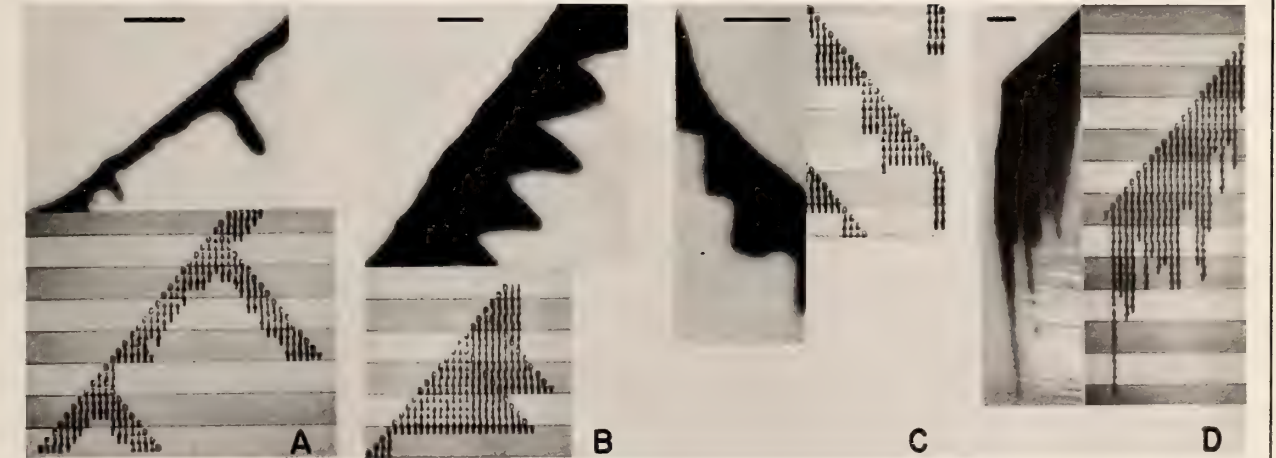


Figure 2

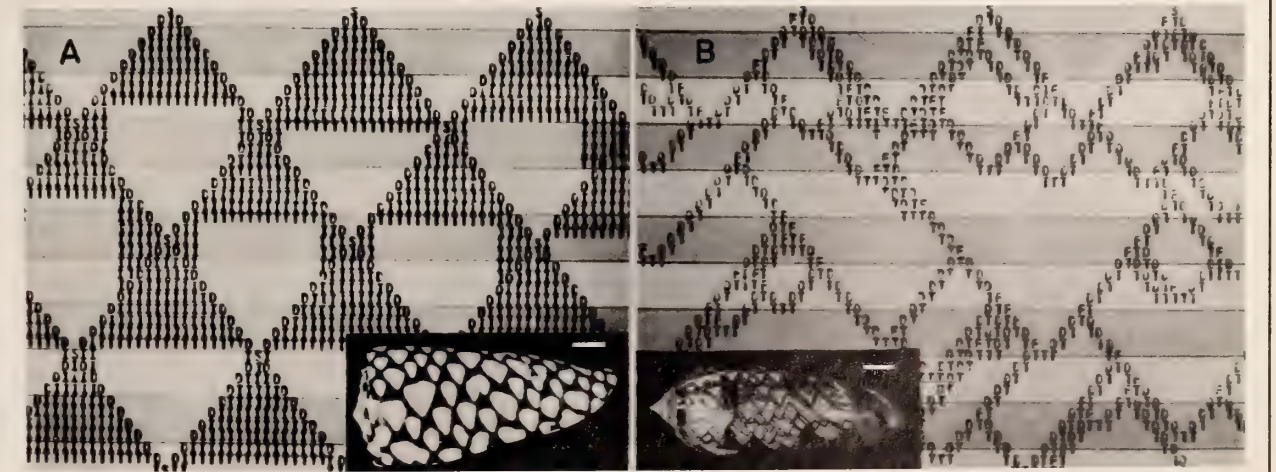


Figure 3

lines branch when they intersect (printed as "s") and moderately long radial lines terminate as in halved patterns. The effect is a network of isosceles triangles which resemble the shell pattern remarkably well.

DISCUSSION

Shelpat's simulations show that realistic patterns resembling three species from three families and two classes of molluscs can be assembled from vertical and diagonal lines. This result suggests that we may be able to improve our understanding of shell pigment pattern diversity by looking for relationships between radial and divergent lines in many different molluscs. The simulations have incorporated four such relationships into the control variables of Shelpat by reducing patterns to common constituents and reassembling them into species-like simulations. Reduction and reassembly are useful because they force the analyst to identify controls that are necessary for acceptable simulation and, by extrapolation, development. Since the lines are on or off, radial or divergent, anterior or posterior, these controls resemble the action of regulatory genes in other binary systems which control sex differentiation in mammals (OHNO, 1971), compartment segregation in imaginal discs of *Drosophila* (MORATA & LAWRENCE, 1978), and shell pigment patterns in *Cepaea* (CAIN, SHEPPARD & KING, 1968; MURRAY, 1975), and *Mercenaria* (CHANLEY, 1961). Modeling with vertical and diagonal lines thus suggests how regulatory genes, that in some views may store answers to the problem of speciation (AVISE, 1976; VALENTINE & CAMPBELL, 1975; CHERRY, CASE & WILSON, 1978; STANLEY, 1979), may control intra- and interspecific pattern variation.

Acceptable reassembly does not prove that patterns have been reduced to their correct constituents. The test of the subunitary basis of shell pigmentation is whether radial and divergent lines appear within the units of patterns. It is evident in *Oliva porphyria* that divergent lines make up most of the pattern, but one cannot exclude the possible existence of radials. Similarly, *Conus marmoreus* occasionally connects triangles with radial and divergent lines, but the triangular units examined so far do not reveal radial lines within. These points need further study to establish whether *O. porphyria* and *C. marmoreus* build patterns according to *Lioconcha* rules.

It appears possible to use control values from Shelpat's simulations to express pattern diversity, but more species

and variables are needed to establish the range of variation. Short of that, it is possible to interpret with certainty preliminary cluster analyses that place less distance between simulations of *Oliva* and *Conus* than between open and halved patterns of *Lioconcha*. Has a small portion of pattern variety been sampled or a large one?

ACKNOWLEDGMENT

I thank Dr. Keith R. Billingsley and Thelma Richardson for help and criticism with Shelpat. This project was supported with research funds from the Department of Zoology, University of Georgia.

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Rondeletiola minor (Naef, 1912)

(Cephalopoda : Sepioidea)

New Record for the Central East Atlantic

BY

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(2 Text figures)

TWELVE SPECIMENS of *Rondeletiola minor* (Naef, 1912) have been collected during the ATLOR VI survey off NW Africa on the research ship "Cornide de Saavedra" in October 1975.

Gear type: bottom trawl

Mesh size: 30 mm in the cod end and 10 mm in cod end cover

Position: 25°15' N-25°48' N, initial and final latitudes, and 15°27' W

Depth: 340-365 m

Type of bottom: sand

Temperature: 13-14° C

Salinity: 35.95-35.79‰ (MANRIQUEZ & RUCABADO, 1976)

The characteristics of specimens collected agree with the descriptions of NAEF (1923) and ADAM (1952).

The material comprises six females ranging from 10 to 14.5 mm dorsal mantle length and six males from 10 to 15 mm DML. Some of the males and females (13-15 mm sizes) were mature. In Figures 1 and 2 the beak and radula of a male of 10 mm DML are shown.

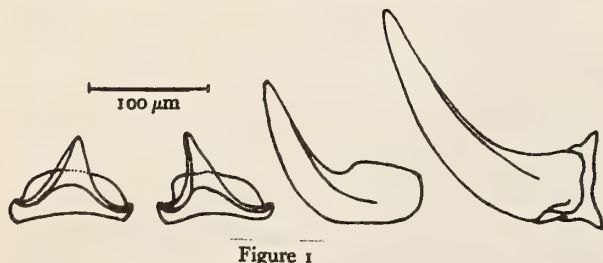
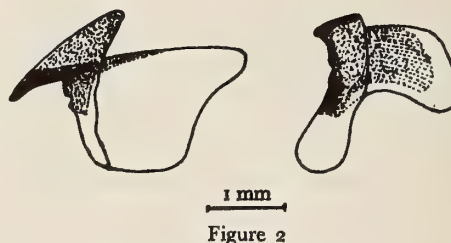


Figure 1

Radula of a male *Rondeletiola minor* of 10 mm DML



Beak of the same specimen

This is the first time that *Rondeletiola minor* has been recorded from this part of the Atlantic. It occurs in the North Atlantic, as proved by a specimen which CHUN (1914) named "*Sepiola rondeleti*" (vide NAEF, 1923). DEGNER (1925) collected a male of 15 mm DML off the coast of Portugal (37°37' N and 10°17' W). ADAM (1952) reported taking 2 males and 3 females from 6 to 12.7 mm DML off the South African coast; three of these were caught between 34 and 150 m depths, and the other two were attracted by light at the surface. PÉREZ-GÁNDARAS (1980) reported taking specimens near the Galician coast (NW of Spain) at 100-200 m depth off the Ria of Vigo.

NAEF (1923) states that *Rondeletiola minor* occurs in the Bay of Naples (Mediterranean Sea) at a depth of 150-200 m on mud and fine sand, that it appears in masses (about 5000 specimens were caught on one occasion) and that it is the most common species of Sepiolidae in the area. WIRZ (1958) reports a male fished at Blanes (Catalonian Sea in the Mediterranean) in 1957, that was exam-

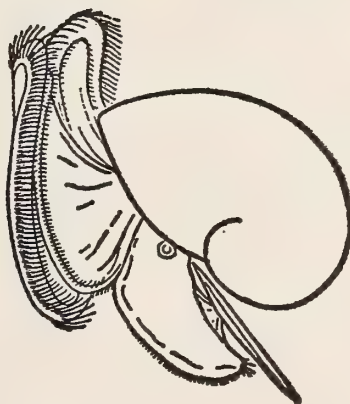
ined by MORALES (1962), who found the specimen in poor condition. A male without spermatophores caught between 400-600 m depth and an immature female collected between 550-640 m in the Port-Vendres region were examined by MANGOLD-WIRZ (1963), who noted that *R. minor* is a rare species in the Catalanian Sea. It occurs also south of Sicily: ADAM (1966) reported two males of 15 and 17 mm DML that were collected SW of Lampedusa island at 42 fathoms [75.6 m] depth, and to the north of Malta at 110-120 fathoms [198-216 m]. BONNET (1973) cited it off the Libyan and Tunisian coasts, and LUMARE (1974) cited a mature male captured at 90 m depth on a muddy bottom in the Tyrrhenian Sea, associated with *Sepiolo ligulata* and *Sepietta oweniana*.

The only place that this species has been found abundantly is in the Bay of Naples. In the other areas cited it seems to be rare, but I think that, because of the small size and behaviour of the species, it has not been well sampled with the gear used.

The distribution of *Rondeletiola minor*, on the basis of present knowledge, includes the Central and Western Mediterranean Sea and the entire Eastern Atlantic, from NW of Spain to South Africa.

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Risk, Reward, and the Duration of Feeding Excursions by a Marine Snail

BY

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(5 Text figures)

INTRODUCTION

THE INTERTIDAL ORGANISMS of rocky shores are periodically exposed to two different media, air and water. Each exposure to air interrupts their feeding and other activities, and while exposed they may become overheated or dehydrated. During the exposure, movement is restricted, and birds, mammals, and crabs take advantage of the low tide periods to hunt their immobile prey. Thus, life in the intertidal zone entails many risks that would not be encountered in the subtidal area.

Some intertidal organisms respond to these risks by migrating up and down the shore. Since the exposure time is a function of height above mean lower low water (MLLW; Figure 1), an organism can minimize exposure time by migrating to the lower shore during low tides and returning to the upper shore to feed during high tides. However, each migration is accomplished at high tide, during the potential feeding time. Moves made at the expense of potential food intake clearly have some disadvantages. As an alternative the organism could remain in the feeding zone continuously, or could find crevices or other protected places near the food supply and move to and from these crevices each day.

Thais lamellosa (Gmelin, 1791) and *T. emarginata* (Deshayes, 1839) are rocky shore snails that move up and down the shore. However, these snails do not make regular daily movements with the tides. Based on risks and food supplies, EMLÉN (1966) predicted that fewer *T. emarginata* would remain on the tops of boulders (where the food was) on warm or sunny days, very stormy days, or days with long tidal exposures. Emlén confirmed these trends for *T. emarginata*, and indicated that movements of *T. lamellosa* are similar.

EMLÉN's (1966) observations suggest that feeding excursions of *Thais lamellosa* should change in response to

changing patterns of risk and reward. At the present study site, on San Juan Island, Washington, the snails feed primarily on the barnacle *Balanus glandula* Darwin, 1854 (SPIGHT, 1981). Barnacles settle throughout the summer, and food quality increases as these barnacles become more numerous and grow. As the summer progresses, low tide exposures become less stressful because the lower tides are higher and occur further from midday. To observe the effects of these temporal changes in risk and reward, I compared feeding behavior during a midsummer and a late summer tidal series.

The following specific questions were asked: (1) are feeding excursions of *Thais lamellosa* more frequent at some stages of the tidal cycle than others, (2) do snails move to hiding places at about the same level as the food supply rather than take longer journeys onto the lower shore, (3) is feeding more frequent in August (when risk is less and reward greater) than in July, and (4) do snails that take longer excursions die sooner? With these questions in mind, daily censuses were taken on a feeding area high in the intertidal zone at Shady Cove, near Friday Harbor, Washington, during two tidal cycles in July and August, 1969.

STUDY AREA AND METHODS

The site, Shady Cove, is about 1 km north of Friday Harbor Laboratories and includes 40 m of shoreline. The steep shore includes only about 5 m of surface between 1.8 m and -0.3 m above MLLW. Most *Thais lamellosa* on this site bore individually numbered tags (SPIGHT, 1974).

Regular censuses were conducted on the whole study area to obtain data for growth and movement studies. Three of these censuses were taken during the activity study period: on 26 June, 11-12 July, and 25 August, 1969.

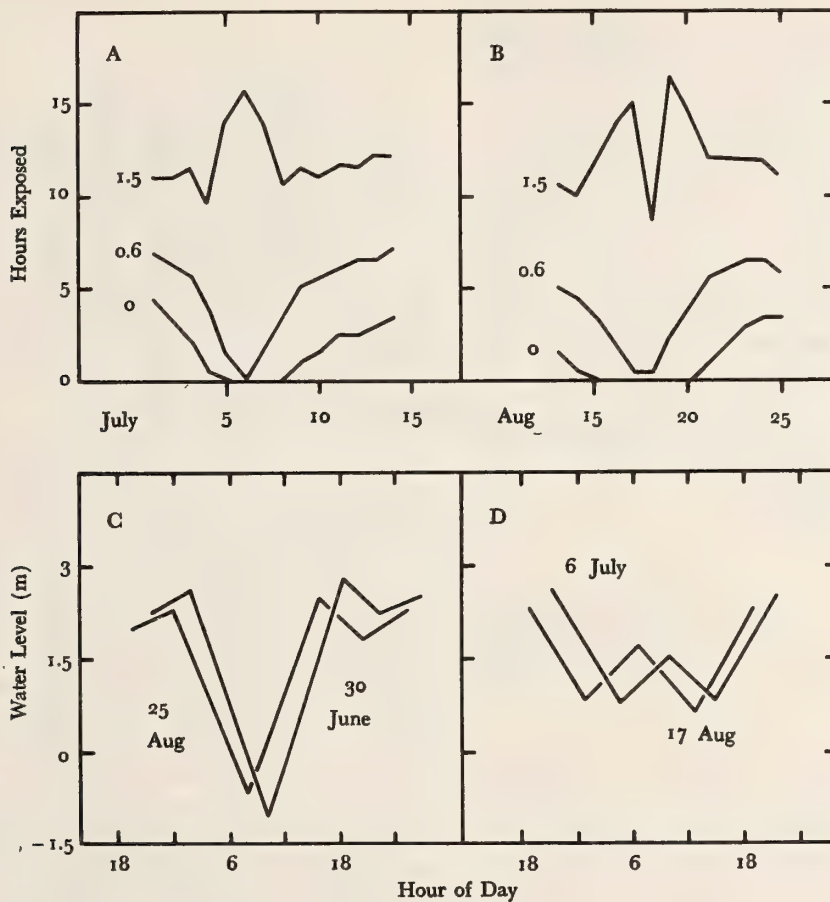


Figure 1

Characteristics of the tidal regime in the Strait of Juan de Fuca, Washington, during the study period, July - August 1969. A and B give the number of hours of exposure on each day at levels of

1.5 m, 0.6 m and 0 m above mean lower low water. C and D give tidal curves for the days with the lowest and highest lower low tides during the study period. Data are from TISON (1969)

Each of these censuses involved a thorough search of the whole study area, which included turning stones and removing snails from crevices. Census data included the tag number of each snail and its location to the nearest 1 m² based on a permanent 1 m x 1 m grid marked on the rocks of the whole study area. On the 26 June and 25 August censuses, all snails were left where they were found, and were disturbed only as much as necessary to determine their identities. On the 11 July census, all snails were removed to the laboratory (to be measured for growth studies). These snails were returned on 12 July.

Special censuses were taken July and August 1969, to reveal the searching behavior of the snails. These activity censuses were designed to identify snails that had been actively foraging during the previous immersion period.

Snails that were on flat surfaces with barnacles were considered to have been foraging. The locations of all such snails were noted each day, 1-9 and 11 July, and 13-17 and 23-25 August. Snails in crevices were assumed to have been inactive, and their numbers were not taken. Positive locations for these would have been helpful, but it was rarely possible to read the numbers without disturbing the snails, and regular disturbance would probably have affected the behavior of the snails. The activity censuses for 11 July and 25 August were made prior to the regular censuses. The terms "active snails" and "snails on the feeding area" refer only to those snails on the flat surface with barnacles. The "feeding area" does not include the crevices and hiding places which are contiguous with the flat surfaces.

All censuses were taken at low tide, and as the lowest low tide of the day became higher and higher, the accessible area decreased. Only one portion of the Shady Cove site was high enough to have been searched completely on most of the dates (except 6 July and 17 August) and also included a large enough number of snails for meaningful analysis. This area, 3 m deep and 8 m long, and between 0.4 m and 1.8 m above MLLW, is designated the "feeding area." Most activity was on a 3 m x 2 m subarea 0.6 m above MLLW. The less complete observations from other areas were used to determine the fates or sources of snails that moved onto or off the feeding area during the study period.

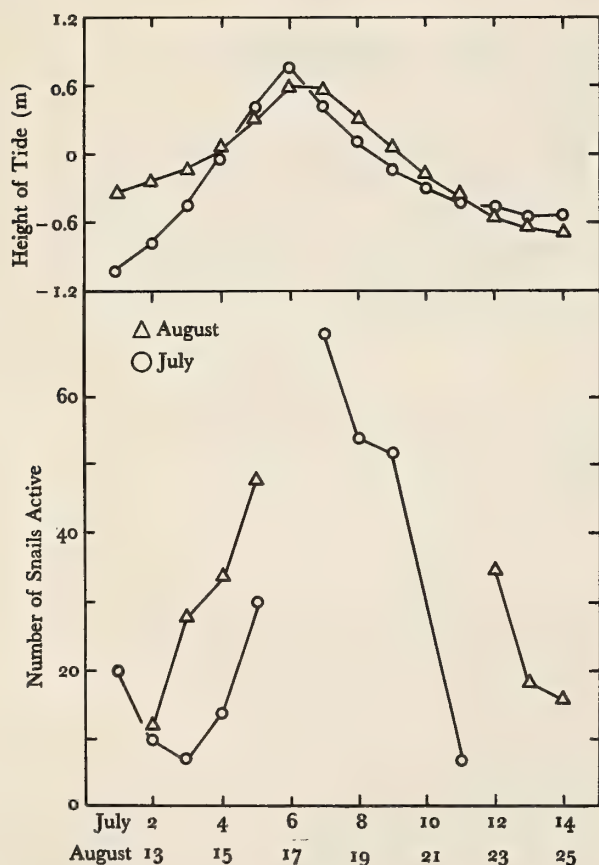


Figure 2

Number of snails on the feeding areas during tidal cycles in July and August 1969. The height of the lowest low tide during each day is plotted in the upper figure. The dates are aligned so that the days of least exposure of each series coincide

RESULTS

Overall Patterns of Activity

Snail activity changed markedly during the tidal cycle. Many more snails were on the feeding areas when tidal excursions were moderate than when they were extreme (Figure 2). However, tidal exposure was not the only factor influencing snail activity. More of the snails were active in August than on comparable tides during July. Also, for a given lower low tide height, many more snails were active when lower low tide heights were increasing on successive days than when they were decreasing (Figure 2).

Behavior of Individual Snails

In total, 159 snails were active (found on the feeding area) on at least one day. However, the average snail was active on only a few of the days. Only 114 snails were found on the feeding area during July, and only 91 during August. Half of the snails were active on only one or two of the 18 census days (82 of 159 snails; Figure 3). Snails that were active during one period were usually inactive during the other period. Of the 159 snails, 127 had been tagged at the beginning of the study period and were still alive at the end. Most of these (86 of 127) were seen on the feeding area during only one of the two periods. Although 56 snails spent three or more days on the feeding area during at least one of the two periods, only 11 snails were active on 3 days during both periods.

Individual feeding excursions were generally short. Only half of the snails (74 of 159) were up on the feeding area on two or more consecutive days, although some remained as long as 5 days. Altogether, there were 4 periods of consecutive daily censuses, each lasting from 3 to 5 days (Figure 2). Even though these periods were short, many snails appeared to make more than one trip (from 4% over 3 days to 21% over 5 days). Actual feeding excursions were undoubtedly longer than the censuses indicate, because it was not possible to take censuses when lower low tides were highest and because some snails on the feeding area were overlooked.

Snails that were not stranded on the feeding areas at low tide must have returned to the lower shore or to nearby crevices before the end of the immersion period. The daily censuses did not include snails in the crevices, and therefore the locations of the secreted snails are not known for most census days. However, the locations of most snails are known for 26 June, 11 July, and 25 August

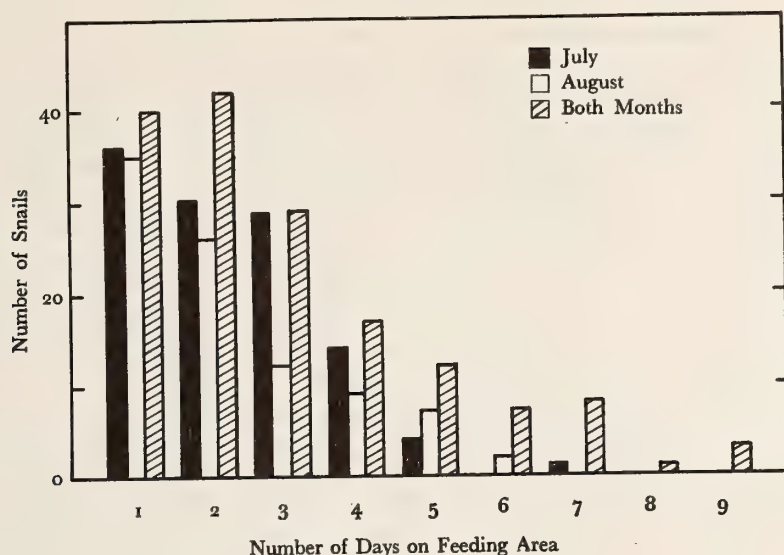


Figure 3

Number of days spent on the feeding area by 159 snails during the July and August, 1969, observation periods, and the total days spent by individual snails during both months

(the beginning and ending of the census periods). These locations can be used to determine how many snails moved vertically. Only 16 of 99 snails (114 less 15 deaths before 11 July) were on the lower shore at the beginning and again at the end of the July census period, while 39 snails made one vertical migration (at the beginning or the end of the period). The remaining 44 snails were on the feeding area or in crevices adjacent to it on both 26 June and 11 July. Observations for the August period are similar (19 snails moved up and down, 30 moved one way, and 31 remained up from 11 July to 25 August; 11 of 91 snails died before 25 August). Therefore, the snails move to and from nearby crevices much more often than they move up and down the shore. Foraging itself may be more frequent than indicated by the censuses because the censuses were taken at low tides and snails may complete foraging trips to and from crevices within each immersion period. However, the censuses do reveal the relative roles of movements to crevices and to the lower shore in the snails' overall behavior pattern.

The snails do make vertical movements frequently. Many of the snails that were seen on the feeding area during only one of the two periods moved up or down the shore. For the August series, 45 new snails moved onto the

feeding area; 18 of these moved from the lower shore, and 6 came from elsewhere on the upper shore. Similarly, 50 snails left the area after July, with 20 of these moving lower on the shore and 13 leaving for other feeding areas. All of the snails collected on 11 July were taken to the laboratory, and later returned to a crevice at the base of the feeding area. Of the 159 snails from the feeding area, 74 were released in this crevice on July 11, and 40 of these later moved up the shore and into the feeding area.

Consequences of Feeding Activity

Snails on the upper shore are exposed to physical stresses for long periods when the tide is low (Figure 1). Since these stresses are a major mortality factor (SPIGHT, 1982), snails making extended feeding trips could well have higher death rates than other snails. Censuses were taken over the entire study area until 1973. These data can be used to identify both long- and short-run fates of the feeding snails (SPIGHT, 1972, 1974). Over the short run, results are opposite those expected; through April 1970, survival was somewhat greater among snails that spent more time in the feeding area (Figure 4). Over the long run, results conform to expectation: snails that spent less time on the upper shore feeding areas during these

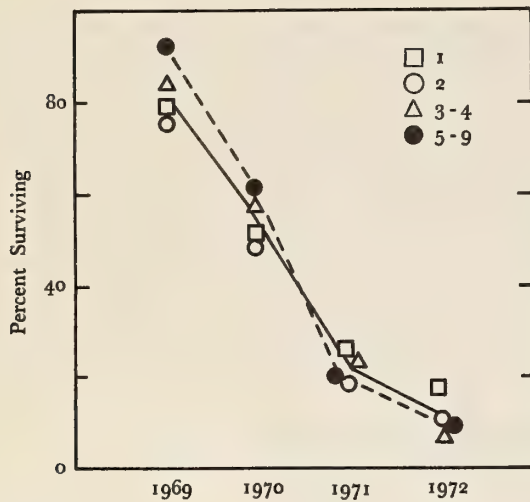


Figure 4

Survival of snails that fed for different amounts of time during July and August, 1969, observation periods. The solid line is the survival for all snails; the dashed line is the survival for the 5-9 day snails

two census periods lived somewhat longer. However, these long-run differences are small and undoubtedly reflect behavior after this study was completed.

DISCUSSION

Each individual snail is faced with a major dilemma: feeding rate can be maximized by staying on the high shore, and risks can be minimized by staying on the low shore. The risks are not trivial; physical stresses are a major cause of death for the Shady Cove snails (SPIGHT, 1982), and moving up the shore into a zone of higher stress bears clear consequences. Likewise, the rewards are often slim. Barnacles are sparse and through much of the year the snails stand to gain little by searching for food (SPIGHT, 1981). Searching and feeding are both time-consuming processes; drilling and feeding require some 2-8 hours per barnacle, and even when allotted a dense barnacle supply under relatively protected field conditions, snails can consume only about 2 barnacles per day (CONNELL, 1970; EMLEN, 1966). Near Friday Harbor, *Balanus glandula* and *B. cariosus* (Pallas, 1788) reach a peak combined density of only about 3/cm² (CONNELL, 1970) between early June and late July (SPIGHT, 1981).

The barnacles gradually disappear from the shore during the summer and fall, and few remain by the time the snails become active in the spring. Despite rapid growth, few of these barnacles live long enough to reach sizes preferred by the snails. With this poor food supply, snails can ill afford to spend potential feeding time merely avoiding stresses. Feeding becomes more risky as the season progresses, because the snails eat the low shore barnacles first, and gradually work their way up the shore as the fall approaches. By spring, the safe lower shore and the remaining upper shore barnacles are often several meters apart.

The complex tidal cycle for the Friday Harbor area adds another dimension to the problem. The behavior of some intertidal organisms is often adjusted closely to such complexities (ENRIGHT, 1972), and one would expect the snails to track the tidal changes closely to minimize stresses. When the lower low tide is highest, the top of the barnacle zone (1.5 to 1.8 m above MLLW) emerges twice a day (Figure 1D), and the dry periods are long (Figure 1A, B). During the lowest low tides, even the mid-shore is exposed for 5 hours or more for several days in succession, and in summer often during the warmest part of the day. These long exposures are followed by the longest immersion periods of the tidal cycle; when the tides are at the extremes there are effectively only two tides per day (Figure 1C). The snails are also exposed progressively later and then earlier in the day as the year proceeds. Near Friday Harbor, the lowest low tides of the year are at mid-day during the warm part of the year and in the middle of the night during the coldest part of the year. During this study, lower low tide times progressed from mid-day in July to early morning in August (Figure 5). Weather effects are superimposed on the relatively predictable tides; a very long tidal exposure could take place on a cool foggy day that presents little stress to the snails, or on a hot dry day that presents very significant stress.

If risk varies so markedly over the tidal cycle, then the optimum behavior for the snail probably varies as well. The risk attending a trip from the lower to the upper intertidal zone is affected by the distance to move, the weather, and the time of exposure, while the reward reflects the density and size of available food items. When the snail often cannot find a barnacle and finish drilling and feeding during a single immersion, risks from predators and physical stresses may outweigh potential gains from foraging. EMLEN (1966) has hypothesized that an individual *Thais emarginata* will leave more offspring if it sits and starves when feeding entails high risks, even though food is "available."

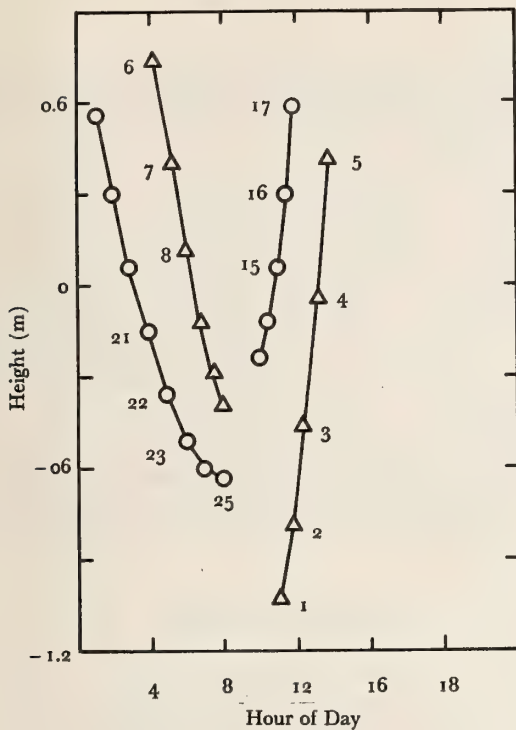


Figure 5

Time and height of lower low tides on 1 - 11 July (Δ) and 13 - 25 August, 1969 (\circ), in the Strait of Juan de Fuca, Washington, from Tison (1969). The numbers are dates

How do the snails solve this problem? Firstly, more snails make feeding excursions during less stressful phases of the tidal cycle (Figure 2). Few snails are active when the tides are lowest, but many are active when the lower low tides are highest. However, activity lags behind the tides. For a given tidal excursion, activity is higher when lower low tide heights are decreasing than when they are increasing (Figure 2). In part, this may reflect the timing of the tides; heights are decreasing when tides are in the morning and weather is often cool and foggy, while heights are increasing when tides are in the afternoon, and the air is often warm and clear (Figure 5). The lags suggest that the snails adjust their activity to actual stresses rather than anticipating the tidal cycle. *Thais emarginata* also responds to actual stresses (EMLEN, 1966).

Secondly, feeding excursions are more frequent during less stressful seasons. More snails made feeding excursions in August than in July (Figure 2). The tidal cycles during these two months differed in both risks and rewards. The

July series fell more toward the middle of the day (Figure 5). On lower low tides of July, water was rapidly evaporated from the intertidal surface and temperature stress must have been significant. The July study period also fell before barnacles reached maximum density. In July, almost all barnacles were small and newly settled. A month later, air temperatures were lower, the tides fell at a less stressful time of the day, and the larger barnacles provided a much more substantial return for drilling and searching effort. Appropriately, many more snails were on the feeding areas during all phases of the census period (Figure 2).

Thirdly, the snails retreat to crevices adjacent to the feeding areas rather than to the lower shore. Active snails typically made short trips into the feeding area, often lasting several days, followed by short trips to nearby crevices. Many snails did make long vertical migrations, but fewer than 25% of them actually made complete round trips from and back to the lower shore during either census period.

The most outstanding aspect of the behavior of these snails is the prevalence of individual differences. Only 41 of 127 snails were active during both census periods. Half of the snails were active on only one or two days of the 8-10 day census periods and activity was scattered throughout both census periods. A few snails moved up and down the shore, a few left for other feeding areas, and others spent their inactive periods in crevices adjacent to the feeding area. Although some days were better than others for activity - based on snail numbers - no day was good enough to draw out a majority of the nearby snails.

Individuals who appeared to take greater risks also survived better in the short run. The benefits of feeding probably outweighed the risks of activity because the snails were in poor condition after several months of low food intake. In the long run, the more active snails did not survive as long (Figure 4). However, it would be premature to interpret this slight long-term difference.

SUMMARY

Thais lamellosa often forages on the upper levels of rocky intertidal shores, and it increases its risk of death from physical stresses and some predators when it does. Studies during two tidal series revealed more frequent foraging as risks decreased and food supplies increased. Snails were more active on the less stressful days of each tidal series and on comparable days of the less stressful tidal series. Some snails spent their inactive time on the lower shore, but most retreated to crevices near the feeding area; thus, they did

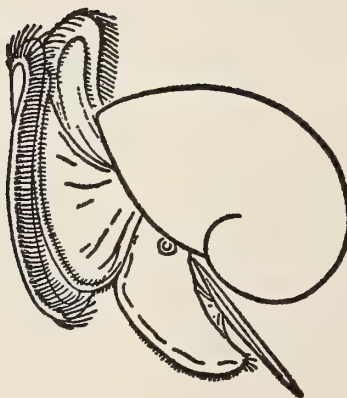
not make daily trips up and down the shore. The net movement was downshore for the lowest low tides of each two-week series, but only 40% of the active snails made a downshore move. Individual differences formed the most prominent aspect of the behavior of these snails. Despite higher stresses in the feeding area, snails spending more time on the upshore feeding areas did not have higher death rates than less active snails.

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A comparative Study of Mollusk Communities on the Shelf-Slope Margin of Barbados, West Indies

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(1 Plate)

INTRODUCTION

THERE ARE FEW COMPREHENSIVE SURVEYS of deep-water mollusks from specific areas of the Caribbean Province which are comparable to those dealing mainly with shallow-water communities (e.g., PEILE, 1926; BENTHEM JUTTING, 1927; ABBOTT, 1958; COOMANS, 1958, 1963; OLSSON & MCGINTY, 1958; USTICKE, 1959; RICE & KORNICKER, 1962; PRINCZ, 1978). The results of early cruises of the *Blake* (DALL, 1881, 1886 and 1889) and more recently those of the R/V *Gerda* and the R/V *John Elliott Pillsbury* (BAYER, 1971) are useful in composing a broad, albeit sketchy, picture, but they lack sufficient detail from any one locality for valid comparisons. Other works have concentrated on specific taxonomic groups, such as the families Trochidae (QUINN, 1979) and Conidae (VAN MOL *et al.*, 1967; VAN MOL, 1973). The studies of TREECE (1980) and RICE & KORNICKER (1965) off the Yucatan Peninsula attempt to combine comprehensive sampling regimes of the deeper water fauna with some relevant environmental factors. Many more such investigations are required before a more complete picture will emerge of the distribution of deep-water mollusks in the Caribbean and of the factors which dictate that distribution.

The principal objectives of the present study were to complement and expand upon LEWIS' (1965) preliminary description of deep-water mollusks (and other invertebrates) off the west coast of Barbados, to determine the relative importance in both biomass and numbers of individual molluscan species, and to provide information on sources of mortality which could be determined by examination of the shells of these species.

ACKNOWLEDGEMENTS

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MATERIALS AND METHODS

Bottom samples were collected from three depths approximating the 125m, the 175m and the 225m contour lines on the shelf-slope margin on the west coast of Barbados. Approximately forty samples were obtained at each depth with a small dredge on the R/V *Martlet*. The contents of each sample were carefully examined, and benthic molluscan species were sorted into three categories—live animals, complete shells, and fragments of shells. Specimens from all three categories were identified to specific level where possible. We have assumed that empty shells and shell pieces collected in a given locality represented species which either inhabit that locality or are found nearby. In the case of empty bivalve shells, the total

number of valves of any one species was halved in order to estimate the number of animals represented. Wet weight was determined by weighing the live animal and shell and subsequently subtracting the weight of the cleaned shell.

Shells of pelagic gastropods which had sedimented onto the sea floor, such as pteropod, heteropod and *Janthina* shells, were not included in our survey; for a description of pteropod sediments in Barbados, see WELLS (1975). The present study also does not attempt to review the systematics of any of the groups encountered, although a manuscript is in preparation describing new and unusual species of the genus *Conus* collected in the study area.

RESULTS

Tables 1-3 list the dominant mollusks which comprised more than 1% of the total live animals and shells at depths of 125, 175, and 225 m, respectively. Table 4 includes all mollusk species which constituted less than 1% of total live animals and shells in at least one of the three study sites. The greatest number of species (Table 4) was obtained from the 175 m depth (198), followed by 165 at 225 m and 112 at 125 m. The total number of mollusk species collected was 278. Although no valid absolute numbers or biomass per unit area of sea bottom can be calculated from sampling with a dredge, visual observations did suggest a strong

positive correlation between density and species diversity at the three sites.

The different depths show obvious differences in species composition. The station at 125 m was dominated by *Nemocardium peramabile* (29.00%, Table 1), whereas *Cerithiopsis crystallinum* dominated the 175 m (28.71%, Table 2) and 225 m (56.90%, Table 3) communities. There were only four species which comprised more than 1% of total numbers at all depths: *Nemocardium peramabile*, *Nassarius scissuratus*, *Olivella watermani*, and *Olivella* sp. B. Interestingly, live specimens of *Olivella* B were never present and it must be assumed that this species forms abundant populations nearby, with the shells being washed onto the shelf-slope area.

Since the data were qualitative, community analysis was limited to calculations of Sorensen's index of similarity for the three component classes of Mollusca present at the three depths (Table 5). The latter were regarded as single stations inasmuch as the various samples collected for each depth were obtained within a relatively small geographic area (fronting the Bellairs Research Institute, St. James) and consequently lumped. Sorensen's Index (or coefficient of community) is defined as $CC = 2a/(2a + b + c)$ where a is the number of species common to the two entities (stations) concerned and b and c are, respectively, the numbers of species found in only the first, and only the second, entity (PIELOU, 1977). The results show the highest similarity between the two deepest stations (175 m and

Table 1
Dominant mollusks collected at 125 m showing comparative numbers, biomass and frequency of boring by predatory gastropods.
(B), bivalves; (S), scaphopods; and *, less than one per cent.

Species	Percentage of total live animals and empty shells	Percentage of total live animals	Percentage of total tissue wet weight	Percentage of bored shells
<i>Nemocardium peramabile</i> (Dall) (B)	29.00	33.47	5.64	5.76
<i>Olivella watermani</i> McGinty	13.12	2.02	*	48.36
<i>Vesicomys vesica</i> (Dall) (B)	6.08	11.29	4.03	5.16
<i>Phos beauit</i> Fisher & Bernardi	6.02	14.92	15.95	31.75
<i>Nassarius scissuratus</i> (Dall)	5.23	*	*	18.82
<i>Olivella</i> sp. B	3.43	0	0	31.82
<i>Nuculana</i> sp. (B)	3.07	2.02	*	0
<i>Dentalium ceratum</i> Dall (S)	2.29	7.66	2.33	0
<i>Conus mindanus</i> Hwass	2.05	2.02	4.62	0
<i>Polystira tella</i> (Dall)	2.05	1.21	1.25	61.29
<i>Siliquaria squamata</i> Blainville	1.99	0	0	0
<i>Microgaza rotella rotella</i> Dall	1.93	*	*	0
<i>Olivella</i> sp. A	1.26	0	0	28.57
<i>Bellaspira pentagonalis</i> (Dall)	1.20	0	0	12.50
<i>Cordieria rouaulti</i> (Dall)	1.00	2.02	*	0

Table 2

Dominant mollusks collected at 175m showing comparative numbers, biomass and frequency of boring by predatory gastropods.
(B), bivalves; (S), scaphopods; and *, less than one per cent.

Species	Percentage of total live animals and empty shells	Percentage of total live animals	Percentage of total tissue wet weight	Percentage of bored shells
<i>Cerithiopsis crystallinum</i> Dall	28.71	38.24	1.40	51.28
<i>Olivella</i> sp. B	13.58	0	0	32.58
<i>Olivella watermani</i> McGinty	11.64	*	*	59.23
<i>Nemocardium peramabile</i> (Dall) (B)	9.60	5.45	1.36	15.01
<i>Vesicomya vesica</i> (Dall) (B)	5.36	7.08	5.38	43.23
<i>Nassarius scissuratus</i> (Dall)	4.71	2.07	*	43.81
<i>Scaphander watsoni</i> Dall	2.59	*	*	0
<i>Polystira tellea</i> (Dall)	1.97	2.51	3.75	75.35
<i>Phos beauui</i> Fisher & Bernardi	1.78	9.26	13.66	57.81

225m) for both Gastropoda and Scaphopoda, but, oddly, between the two extremes (125m and 225m) for Bivalvia. The least similarity for gastropods was, expectedly, between the 125m and 225m sites, but between the 125m and 175m stations for bivalves and scaphopods. If all the mollusks are combined for each depth, calculated similarity indices are strongly influenced by the numerous species of gastropods. The similarity is thus greatest between aggregates at 175m and 225m and least between those at 125m and 225m.

Apart from total number of species, another expression of diversity is the degree to which the species of a com-

munity are equally abundant. This can be calculated as an equitability component (LLOYD & GHELARDI, 1964), but a rough estimate of equitability is the percentage of all species that comprised half the total number of mollusks at each of the three sites. These percentages are 3.51%, 1.44% and 0.60% for the 125m, 175m and 225m depths, respectively. This gradient suggests that the mollusks closer to shore are more evenly divided among the component species than those farther from shore. Furthermore, of the species contributing 1% or more to the total, 15 comprised 91.41% of the total live specimens and 19 constituted 81.33% of all the empty, intact shells collected at

Table 3

Dominant mollusks collected at 225m showing comparative numbers, biomass and frequency of boring by predatory gastropods.
(B), bivalves; (S), scaphopods; and *, less than one per cent.

Species	Percentage of total live animals and empty shells	Percentage of total live animals	Percentage of total tissue wet weight	Percentage of bored shells
<i>Cerithiopsis crystallinum</i> Dall	56.90	41.10	6.72	42.64
<i>Nemocardium peramabile</i> (Dall) (B)	8.90	15.53	11.04	33.81
<i>Olivella</i> sp. A	8.10	1.79	1.36	25.00
<i>Olivella</i> sp. B	3.16	0	0	34.00
<i>Nassarius scissuratus</i> (Dall)	1.77	*	*	31.29
<i>Arene variabilis</i> (Dall)	1.77	*	*	6.06
<i>Olivella watermani</i> McGinty	1.64	0	0	62.34
<i>Olivella rotunda</i> Dall	1.53	2.51	2.71	34.43
<i>Limopsis</i> sp. (B)	1.46	13.26	1.52	0
<i>Dentalium gouldii</i> Dall (S)	1.20	2.15	1.54	31.91

Table 5

Indices of similarity for combined mollusks
and component classes
at the 125 m, 175 m and 225 m depths

	125 m - 175 m	125 m - 225 m	175 m - 225 m
Gastropods	0.522	0.471	0.559
Bivalves	0.558	0.654	0.607
Scaphopods	0.500	0.546	0.800
Combined spp.	0.532	0.504	0.576

125 m. Comparable figures are 19 species and 88.63% for live animals and 13 species and 82.90% for shells at 175 m, and 13 species and 92.22% and 9 species and 87.48% for live animals and shells, respectively, at 225 m. It is clear, therefore, that relatively few species dominate numerically in the communities at all three depths. However, as demonstrated in the tables, the contributions of dominant species to total biomass are relatively low, reflecting their small sizes (e.g., *Cerithiopsis crystallinum*).

Tables 1-4 also provide some insight into mortality caused by the predation of boring gastropods. It is clear from the high percentages of shells with cylindrical drill holes, that attrition through boring activities of drills can play an important role in the communities. Of the 21 dominant species listed in Tables 1-3, only three show no evidence of boring. One, *Scaphander watsoni*, is an opisthobranch with a thin external shell which is unable to contain the whole body during retraction. Thus the animal is easily available to predators without boring. The other two species (*Nuculana* sp. and *Limopsis* sp.) are very small bivalves, and their small size and burrowing habits may give them a refuge from boring gastropods. The remaining 18 dominant species all show evidence of predation by borers, with the percentages of bored shells ranging from 2.86% (*Siliquaria squamata* at 225 m) to 75.35% (*Polystira tellea* at 175 m). Those species with more than 18% of shells bored at all 3 depths are: *Phos beauui*, *Polystira tellea*, *Cerithiopsis crystallinum*, *Nassarius scissuratus*, *Olivella* sp. A, *Olivella* sp. B, and *Olivella watermani*. If one includes *Olivella rotunda*, which is not present at 125 m but has a high percentage of bored shells at 175 m (28.57%) and at 225 m (34.43%), it is obvious that the four species of *Olivella* contribute significantly to the diets of drills, as do the four unrelated gastropods listed above. In fact, few of the mollusk species for which we have sufficient data (Table 4) appear to escape the predatory activities of drills, including the drills themselves. Species belonging to the genera *Cymatium*, *Distorsio*, *Morum*, *Murex*, *Natica*, *Phalium* and

Polinices, as well as others, are suspected of being capable of drilling into prey shells.

Examination and identification of shell pieces and fragments in the dredge samples were undertaken for two reasons. First, this exercise confirmed the presence of certain species in areas where no whole specimens, dead or alive, were observed from the samples. Second, the information also served to indicate the extent to which specific species appear to have been preyed upon by such molluscivores as octopi, crabs and fish, including rays. In this connection, bivalves especially were prone to shell breakage. Larger *Dentalium* species and numerous gastropods, particularly cones like *Conus mindanus* and *C. mazel*, also met their fate this way. Other species with predation related breakage included *Tugurium caribaeum*, *Olivella* spp., *Siliquaria* spp., *Phos beauui*, *Murex caillieti*, *Evokesia grayi* and *Natica castrensis*. In addition, a very high percentage of intact shells, particularly of cones, had mutilated lips, which suggests attacks on the live animals. It is tentatively concluded, therefore, that predation mortality is very high in the mollusk populations at the study sites.

DISCUSSION

The total number of molluscan species collected (278) can be compared favourably with the 227 species collected by LEWIS (1965) from depths between 50 m and 400 m in the same general area. The significantly greater number of species, particularly of gastropods, obtained in the present study undoubtedly reflects the fact that approximately twice as many dredge samples were taken. Additional samples would likely add more species, but these would be rare locally and not constitute a numerically important element in the molluscan community. Many of the species already collected, as seen in Table 4, were represented by single specimens only. In contrast to LEWIS' (1965) data, which showed declining numbers of species with depth from 100 m to 250 m, our results indicate the lowest species diversity at 125 m, the highest at 175 m, followed by a decrease of 225 m. The attenuation in diversity of molluscs with depth has also been observed on the Yucatan shelf, where TREECE (1980) obtained 339 species and RICE & KORNICKER (1965) collected 175 species between approximately 30 m and 500 m.

The findings of certain species deserve comment. A number of small shells could not be identified and require further work. Some of these may be new species. Others, such as *Conus huntii* and *Conus sanderi* WILS & MOOLENBECK, 1979) and *Sassia lewisi* (HARASEWYCH & PETUCH, 1980) have been described recently from specimens collected in the present study. Some species regarded as rare also were

collected. These included *Ficus howelli*, *Bathytoma viabrunnea* (Figure 1), *Morum dennisoni*, *Cypraea surinamensis* (encrusted and damaged), *Poirieria hystricina*, *Conus cedonulli* and *Puncturella (Fissurisepta) cf. trifolium*, the latter otherwise known only from Dall's (1881) holotype from the Yucatan Straits, Mexico. *Fusinus ceramidus* (Figure 1), thus far collected off Barbados only (DALL, 1889; LEWIS, 1965), was sampled in small numbers, but *Phos beauii*, of which BAYER (1971) found only one specimen off St. Vincent, was not uncommon. In addition, fragments of *Perotrochus adansonianus* and *P. quoyanus* were sampled on the rubble bottom at 175m. In this connection, Barbados is considered a classic pleurotomarian locality from which *Perotrochus adansonianus*, *P. quoyanus* and *P. gemma* previously have been collected (BAYER, 1965, 1967) in the rough bottom typically inhabited by this group. An array of species usually associated with West Indian inshore coral reefs, rubble bottoms or *Thalassia* beds were clearly adapted to living in deeper waters as well. Live specimens of *Cypraea cinerea*, *C. spurca acicularis*, *Oliva reticularis* and *Polinices lacteus* were collected from our study sites. Other shallow-water species, such as *Cypraecassis testiculus*, *Bursa thomae* and *Voluta musica* were represented by shells only; such species probably do not form part of the living molluscan fauna in deeper waters.

The results of classification of communities (Table 5) indicate that deep-water molluscan communities, although separated by relatively short geographic distances, may nevertheless show distinct qualitative differences. These differences may arise from variation in substratum, attendant fauna (including potential predators and prey), depth, and distance from shore. The latter two factors imply differences in biological, chemical and physical variables of the overlying waters. For example, BEERS *et al.* (1965) reported an average drop of 10°C between 100m and 250m off the west coast of Barbados. In this connection, it is possible that some of the mollusks in the present study are stenothermic and their depth distribution thus limited by temperature. Salinity, on the other hand, remained unchanged, so that even stenohaline organisms are unlikely to be affected by this factor. However, the high percentage contribution by filter-feeding bivalves at the 125m station compared to the two deeper stations (Tables 1, 2 and 3) may reflect the expected relative richness in particulate organic matter of the overlying waters at 125m. The latter probably fall within the lower limits of the plankton-rich photosynthetic zone, and, being closer to shore, undoubtedly reflect the benefits of the "island-mass" effect—demonstrated for Barbados by SANDER & STEVEN (1973), SANDER (1976), and SANDER & MOORE (1978). Visual observations of the sediments obtained in the dredge hauls indicated that in many places the bottom at the 125m level was uniformly sandy. By contrast, deeper-water hauls con-

tained more rubble and attendant non-molluscan fauna. LEWIS' (1965) analysis of bottom sediments on the west coast corroborate these findings. Two of his sampling depths approximate ours, and show that at 134m (\approx 125m) only 3.9% of the total sample weight was greater than 1.651mm, compared to 12.6% at 225m. In addition, organic carbon comprised only 0.19% at 134m but 2.25% at 225m. The above may dictate the lower species diversity at the shallow depth and the high incidence of filter-feeders (exemplified by the dominant bivalve, *Nemocardium peramabile*), contrasted to the higher species diversity and preponderance of deposit feeders (exemplified by the dominant gastropod, *Cerithiopsis crystallinum*) at the deeper sites.

Developmental patterns of deep-water mollusks of the area are generally unknown and most planktonic veligers have not been identified; consequently, the importance of larval dispersal in determining distribution patterns remains uncertain. Nevertheless, for those mollusk species with pelagic larvae, there is the possibility of exchange with more remote islands or land masses as well as the possibility of retention of larvae within the Barbados shelf area. Although the prevailing equatorial current flows from the Atlantic Ocean past Barbados and into the Caribbean Basin (WÜST, 1964; JOHANNESSEN, 1968), EMERY (1972) has postulated the existence of vortices on the leeward side of the island which could function as retaining mechanisms for meroplanktonic larvae. Also, the results of GLOMBITZA (1971), MAZEIKA (1973), and ORTEGA & HERRERA (1976) present a picture of a very complex situation of eddies and counter-eddies, of flows as often easterly as westerly. MAZEIKA (1973) regarded this as evidence of water flowing from the east piling up against the Lesser Antilles and washing back to the east. This phenomenon, coupled with the intrusion in the region of Barbados of water masses originating off the coast of South America (STEVEN & BROOKS, 1972; KIDD & SANDER, 1979), could render the Barbados marine Mollusca less isolated than cursory inspection of a geographic map may indicate. This assumes that some pelagic larvae originating in South America or adjacent Windward Islands, such as St. Lucia and St. Vincent, are able to delay metamorphosis until they reach waters overlying the shelf-slope margin of the island.

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Table 4

Species comprising less than 1% of total mollusk members in at least one depth.

L, includes living animals; S, intact shells;

F, shell fragments only; 1, single specimen only;

*, percentage of total tissue wet weight if more than 1%.

Species	Presence at			
	125 m	175 m	225 m	
GASTROPODA				
PLEUROTOMARIIDAE				
<i>Perotrochus adansonianus</i> (Crosse & Fischer)		F		
<i>Perotrochus quoyanus</i> (Fischer & Bernardi)		F		
FISSURELLIDAE				
<i>Diodora</i> sp.		1,S	1,S	
<i>Diodora cayenensis</i> (Lamarck)	S		S	
<i>Diodora listeri</i> (Orbigny)		S		
<i>Diodora sayi</i> (Dall)	S	S		+
<i>Emarginula tuberculosa</i> Libassi		S	S	
<i>Lucapina suffusa</i> (Reeve)		L	1,S	
<i>Puncturella (Fissurisepta) cf. trifolium</i> Dall			1,S	
COCCULINIDAE				
<i>Cocculina portoricensis</i> Dall & Simpson			1,S	
LEPETELLIDAE				
<i>Addisonia</i> sp.			S	
TROCHIDAE				
<i>Calliostoma</i> sp. A		F	1,S	
<i>Calliostoma</i> sp. B		L		+
<i>Calliostoma fascians</i> Schwengel & McGinty	1,S			
<i>Calliostoma jujubinum</i> (Gmelin)	1,S			
<i>Calliostoma marionae</i> Dall		S		+
<i>Calliostoma olsoni</i> Bayer			1,S	
<i>Calliostoma pulchrum</i> (Adams)	1,S	1,S		
<i>Calliostoma roseolum</i> Dall		S		+
<i>Calliotropis</i> sp.		1,S		
<i>Euchelus dentifera</i> (Dall)			S	+
<i>Gaza (Gallogaza) watsoni</i> (Dall)	1,L	1,L		
<i>Lischkeia imperialis</i> (Dall)		1,S		
<i>Microgaza rotella</i> Dall	Table 1			+
<i>Solariella asperrima</i> (Dall)		S		
<i>Solariella lacunella</i> (Dall)	L	L	L	+
CYCLOSTREMATIDAE				
<i>Arene variabilis</i> (Dall)	1,S		Table 3	+
TURBINIDAE				
<i>Homalopoma</i> sp.			1,S	
<i>Liotia bairdii</i> (Dall)			1,S	
SILICULARIIDAE				
<i>Siliquaria modesta</i> Dall		S	S	
<i>Siliquaria squamata</i> Blainville	Table 1	S	L	+

Table 4 (Continued)

Species	Presence at			Evidence of predation by boring (+)
	125 m	175 m	225 m	
ARCHITECTONICIDAE				
<i>Architectonica peracuta</i> (Dall)		S		+
<i>Heliacus</i> sp.	1,S			+
<i>Heliacus bisulcatus</i> (Orbigny)			1,S	
<i>Heliacus sigsbeei</i> (Dall)			1,S	
CERITHIIDAE				
<i>Cerithiopsis</i> sp.		1,S		
<i>Cerithiopsis crystallinum</i> Dall	S	Table2	Table3	+
<i>Cerithium litteratum</i> (Born)		F		
EPITONIIDAE				
<i>Amaea retifera</i> (Dall)		1,S	S	
<i>Cirsotrema pilsbryi</i> (McGinty)		S	S	
<i>Opalia pumilio morchiana</i> (Dall)	1,L	L		
<i>Sthenorytis pernobilis</i> (Fischer & Bernardi)		F		
MELANELLIDAE				
<i>Eulima</i> sp.		S		
<i>Niso aeglees</i> Bush	S	L	L	+
ATLANTIDAE				
<i>Atlanta peronii</i> Lesueur		1,S		
FOSSARIDAE				
<i>Fossarus bellus</i> (Dall)			1,S	
CREPIDULIDAE				
<i>Cheilea</i> sp.	S		S	
<i>Cheilea equestris</i> (Linnaeus)		S		
XENOPHORIDAE				
<i>Tugurium caribaeum</i> (Petit)	S	S	S	+
ERATOIDAE				
<i>Trivia</i> sp.	1,S			
<i>Trivia candidula</i> Gaskoin	L		S	+
CYPRAEIDAE				
<i>Cypraea cinerea</i> Gmelin	S	L	1,S	
<i>Cypraea spurca acicularis</i> Gmelin		L		
<i>Cypraea surinamensis</i> Perry	F			
OVULIDAE				
<i>Cyphoma gibbosum</i> (Linnaeus)			F	
<i>Cyphoma intermedium</i> (Sowerby)	F	1,S		
<i>Primovula carnea</i> (Poiret)		L		
<i>Pseudosimnia pyrifera</i> Gate		S		
NATICIDAE				
<i>Natica</i> sp. A		S		
<i>Natica</i> sp. B			L	
<i>Natica</i> sp. C			S	
<i>Natica castrensis</i> Dall	1,S	L,4.38*	1,L	+
<i>Natica cayennensis</i> Récluz		F	1,S	+
<i>Natica perlineata</i> Dall	1,S	S	L	+
<i>Natica livida</i> Pfeiffer	1,S	S	S	+
<i>Polinices</i> sp.			L	
<i>Polinices lacteus</i> (Guilding)	F	L,1.43*		+
<i>Sinum minor</i> (Dall)		1,S	S	

Table 4 (Continued)

Species	Presence at			Evidence of predation by boring (+)
	125 m	175 m	225 m	
CASSIDAE				
<i>Cypraea testiculus</i> (Linnaeus)	F	F		
<i>Morum dennisoni</i> (Reeve)	F	L, 1.05*	1, L, 11.36*	+
<i>Phalium</i> sp.			F	
<i>Phalium granulatum</i> (Born)		S	F	
<i>Sconsia</i> sp.		F		
CYMATIIDAE				
<i>Charonia variegata</i> (Lamarck)		F		
<i>Cymatium moritinctum caribbaeum</i> Clench & Turner	S			
<i>Cymatium testudinarium rehderi</i> Verrill		1, L		
<i>Distorsio clathrata</i> (Lamarck)		1, S		+
<i>Distorsio constricta mcgintyi</i> Emerson & Puffer	L, 5.79*	L, 12.37*	S	+
<i>Sassia lewisi</i>				
Harasewych & Petuch		S		
BURSIDAE				
<i>Bursa thomae</i> (Orbigny)	1, S			
TONNIDAE				
<i>Eudolium thompsoni</i> McGinty		S	S	+
FICIDAE				
<i>Ficus howelli</i> Clench & Aguayo	1, S	1, S	1, S	
MURICIDAE				
<i>Evokesia grayi</i> Dall	L	L	S	+
<i>Murex caileti</i> Petit	L, 12.74*	L, 8.19	S	+
<i>Murex consuelae</i> Vokes	L, 3.04*	1, L		
<i>Murex hidalgoi</i> Crosse		1, S	1, S	+
<i>Murex motacilla</i> Gmelin	1, S			
<i>Poirieria hystricina</i> Dall			L	
<i>Poirieria stimpsonii</i> (Dall)		1, S		
CORALLIOPHILIDAE				
<i>Coralliophila</i> sp.		1, S		
<i>Coralliophila lintoni</i> (Verrill)			1, S	
<i>Coralliophila aberrans</i> (C. B. Adams)		1, S		
<i>Latiaxis</i> sp. A			S	
<i>Latiaxis</i> sp. B		S		+
<i>Latiaxis</i> sp. C		1, S		
<i>Latiaxis dalli</i>				
Emerson & D'Attilio	1, S	L	S	+
<i>Latiaxis mansfieldi</i> (McGinty)	L	1, S		
COLUMBELLIDAE				
<i>Anachis</i> sp.	1, S	F		
<i>Cosmioconcha calliglypta</i> (Dall & Simpson)	1, S	L		+
BUCCINIDAE				
<i>Buccinidae</i> sp.			1, S	
<i>Colubraria</i> (<i>Monostiolum</i>) sp.	1, S	1, S		+
<i>Colubraria swifti</i> (Tryon)	S	L	S	+
<i>Engina caribbaea</i>				
Bartsch & Rehder		S	1, S	+
<i>Phos beauii</i> Fisher & Bernardi	Table 1	Table 2	L, 8.43*	+

Table 4 (Continued)

Species	Presence at			Evidence of predation by boring (+)
	125 m	175 m	225 m	
NASSARIIDAE				
<i>Nassarius</i> sp. A		1,S		
<i>Nassarius</i> sp. B			1,S	
FASCIOLARIIDAE				
<i>Dolicholatirus pauli</i> (McGinty)		S		
Fasciolaridae sp.		S		
<i>Fusinus ceramidus</i> (Dall)	S	L	L	+
<i>Fusinus closter</i> Philippi	F	1,S		
<i>Fusinus eucosmius</i> (Dall)	1,S	L		
OLIVIDAE				
<i>Oliva reticularis</i> Lamarck	L,27.10*	S	S	+
<i>Olivella</i> sp. A	Table 1	S	Table 3	+
<i>Olivella fuscocincta</i> Dall	1,S			
<i>Olivella rotunda</i> Dall	1,S	S	Table 3	+
MITRIDAE				
<i>Mitra straminea</i> A. Adams		1,S		
<i>Mitra swainsonii antillensis</i> Dall	L,1.63*	L,11.90*	L	+
<i>Nebularia</i> sp.		S		+
<i>Thala</i> sp.		S	1,S	+
<i>Thala faveata</i> (Sowerby)		L	1,S	
<i>Vexillum</i> sp. A	L			
<i>Vexillum</i> sp. B	1,L	L	1,S	
<i>Vexillum</i> sp. C	1,S	1,S	1,S	
<i>Vexillum hendersoni</i> (Dall)	S	S		
<i>Vexillum laterculatum</i> (Sowerby)		1,S		
<i>Vexillum styria</i> Dall		L	L	+
<i>Vexillum sykesi</i> (Melvill)		1,S	1,S	
VOLUTIDAE				
<i>Voluta musica</i> Linnaeus	F			
MARGINELLIDAE				
<i>Hyalina lactea</i> (Kiener)		S		+
CONIDAE				
<i>Conus</i> spp. (unrecognisable)	S	S	S	+
<i>Conus</i> sp. A	S	L,5.38*	S	+
<i>Conus</i> sp. B		S		
<i>Conus</i> sp. C		S		
<i>Conus attenuatus</i> Reeve	S	L		+
<i>Conus cedonulli</i> Linnaeus	1,L,5.98*	L,2.58*		
<i>Conus centurio</i> Born	F	L	F	
<i>Conus daucus</i> Hwass		L,2.91*		
<i>Conus hunti</i>				
Wils & Moolenbeek	L	L,1.21*	S	+
<i>Conus mazei</i> Deshayes	L	L	S	+
<i>Conus mindanus</i> Hwass	Table 1	L,3.69*	S	+
<i>Conus sanderi</i>				
Wils & Moolenbeek	S	L,2.10*	S	+
TEREBRIDAE				
<i>Terebra</i> sp.		1,S		
<i>Terebra protexta limatula</i> Dall	1,S			
TURRIDAE				
<i>Bathybela nudator</i> (Locard)			1,S	
<i>Bathytoma viabrunnea</i> (Dall)			1,S	



Figure 1

Figure 2

Figure 1: *Bathytoma viabrunnea* (Dall, 1889)

Figure 2: *Fusinus ceramidus* (Dall, 1889)

Table 4 (Continued)

Species	Presence at			Evidence of predation by boring (+)
	125 m	175 m	225 m	
<i>Bellaspira margaritensis</i> McLean & Poorman			1,S	
<i>Bellaspira pentagonalis</i> (Dall)	Table 1	S	S	+
<i>Borsonella</i> sp.		1,L		
<i>Cerodrillia</i> sp. A		S	L	+
<i>Cerodrillia</i> sp. B	1,S			
<i>Cerodrillia perryae</i> Bartsch & Rehder	S	L	1,S	+
<i>Cerodrillia thea</i> (Dall)		1,S	S	+
<i>Cochlespira radiata</i> (Dall)	L	L	L	+
<i>Cordieria rouaulti</i> Dall	Table 1	S		+
<i>Crassispira</i> sp.		1,S		
<i>Crassispira rhythmica</i> Melvill	S	L		+
<i>Cryoturris corallina</i> (Watson)			1,S	
<i>Cryoturris lavelleana</i> (Orbigny)		1,S	1,S	
<i>Cymatosyrinx</i> (<i>Leptadrillia</i>) <i>splendida</i> (Bartsch)	S	L	L	+
<i>Cymatosyrinx pagodula</i> (Dall)		1,S		
<i>Daphnella corbicula</i> Dall		S		
<i>Daphnella eugrammata</i> Dall		S		+
<i>Daphnella grundifera</i> (Dall)			1,S	
<i>Daphnella leucophlegma</i> (Dall)		S	1,S	
<i>Daphnella lynneiformis</i> (Kiener)			1,S	+
<i>Daphnella morra</i> (Dall)			S	
<i>Drillia albicoma</i> (Dall)	S	L	S	+
<i>Drillia tryoni</i> Dall	S	S	L	+
<i>Drilliola</i> sp.		1,S	1,S	
<i>Fenimorea janetae</i> Bartsch		1,S		
<i>Fenimorea halidorema</i> Schwengel		L		+
<i>Glyphostoma</i> sp.		L	1,S	+
<i>Glyphostoma claudeni</i> Dautzenberg	1,S		S	+
<i>Glyphostoma gabbi</i> Dall	L		L	+
<i>Glyphostoma gratula</i> Dall			S	+
<i>Glyphostoma hendersoni</i> Bartsch		1,L	S	
<i>Glyphostoma herminea</i> Bartsch	1,S	S	F	
<i>Glyphostoma thalassoma</i> (Dall)		1,S		
<i>Hindsiclava alesidota</i> (Dall)	1,S	S	S	+
<i>Ithycthyara cymella</i> (Dall)		1,S	1,S	
<i>Ithycthyara lanceolata</i> (C. B. Adams)		L	S	
<i>Leptadrillia cookei</i> (Smith)			1,S	
<i>Mangelia bartletti</i> (Dall)		S	1,S	
<i>Mangelia monocingulata</i> Dall		S	S	+
<i>Microdrillia</i> sp.		1,S		
<i>Micacathurella</i> , n. sp.		S		
<i>Mitrolumna</i> sp.			S	
<i>Mitrolumna biplicata</i> Dall		1,S		
n. gen. n. sp.		1,S		
<i>Pleurotomella circumvoluta</i> (Watson)			1,S	
<i>Polystira tellea</i> (Dall)	Table 1	Table 2	L,5.02*	+
<i>Polystira albida</i>	1,L,1.06*			
<i>Pyrgocythara</i> sp.			1,S	

Table 4 (Continued)

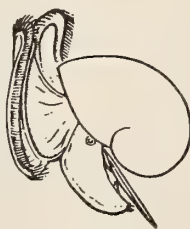
Species	Presence at			Evidence of predation by boring (+)
	125 m	175 m	225 m	
<i>Saccharoturris monosingularata</i> Dall			1,S	
<i>Splendrillia fucata</i> (Reeve)		1,S		
<i>Splendrillia janetae</i> Bartsch	L	L		+
<i>Splendrillia lissotropis</i> (Dall)			1,S	
<i>Splendrillia tantula</i> (Bartsch)	S			
<i>Splendrillia woodringi</i> (Bartsch)		S		
<i>Tenaturris decora</i> (Smith)		S		+
<i>Tenaturris inepta</i> (Smith)			S	+
<i>Triphora</i> , n. sp.	1,S	S		
PYRAMIDELLIDAE				
<i>Pyramidella</i> (Longchaeus) sp.			1,S	
<i>Pyramidella subdolabrate</i> Mörch			S	
<i>Turbonilla</i> sp. A		S	1,S	
<i>Turbonilla</i> sp. B			1,S	
ACTEONIDAE				
<i>Acteon</i> sp. A		S		+
<i>Acteon</i> sp. B		1,S	S	
<i>Acteon delicatus</i> Dall		1,S	L	
<i>Acteon perforatus</i> Dall	1,S	S	+	
<i>Acteon punctostriatus</i> (C. B. Adams)		1,S		
CYCLICHNIDAE				
<i>Scaphander watsoni</i> Dall	L,1.03*	Table 2	S	
HAMINOEIDAE				
<i>Haminoea elegans</i> (Gray)		1,S		
TYLODINIDAE				
<i>Umbraculum</i> sp.		1,S		
SCAPHOPODA				
DENTALIIDAE				
<i>Dentalium</i> sp.		S		
<i>Dentalium callipeplum</i> Dall		S		
<i>Dentalium cardium</i> Dall		1,S	L	
<i>Dentalium ceratum</i> Dall	Table 1	L,1.19*	L,2.14*	+
<i>Dentalium floridense</i> Henderson			L,4.97*	
<i>Dentalium gouldii</i> Dall		1,S	Table 3	+
<i>Dentalium laqueatum</i> Verrill	S	L,3.99*	L,11.51*	+
<i>Dentalium sowerbyi</i> Guilding		S	S	
<i>Dentalium stenochizum</i> Pilsbry & Sharp	L	L	S	
<i>Dentalium taphrium</i> Dall		S	S	
BIVALVIA				
NUCULANIDAE				
<i>Nuculana</i> sp.	Table 1	S	1,S	
<i>Nuculana vitrea cerata</i> (Dall)			S	
ARCIDAE				
<i>Arca polycyma</i> Dall	S	S	S	+
Arcidae sp. A	S	L	S	+
Arcidae sp. B	L		S	
Arcidae sp. C		F	1,S	
<i>Barbatia ectocomata</i> (Dall)		F	L	
<i>Bathyarca glomerula</i> (Dall)			1,S	

Table 4 (Continued)

Species	Presence at			Evidence of predation by boring (+)
	125 m	175 m	225 m	
LIMOPSIDAE				
<i>Limopsis</i> sp.			Table 3	
GLYCYMERIDAE				
<i>Glycymeris pectinata</i> (Gmelin)	F		1,S	
<i>Glycymeris subtilis</i> (Nicol)		S		
MYTILIDAE				
<i>Amygdalum sagittatum</i> Rehder	1,S	L		
PECTINIDAE				
<i>Aequipecten</i> sp. A		S	F	
<i>Aequipecten</i> sp. B	S	S		
<i>Aequipecten phrygium</i> (Dall)	S		S	
<i>Pecten chazaliei</i> Dautzenberg	F			
PROPEAMUSSIIDAE				
<i>Propeamussium pourtalesianum</i> (Dall)	S	S	L	
PLICATULIDAE				
<i>Plicatula gibbosa</i> Lamarck	1,S	1,S		
ANOMIIDAE				
<i>Anomia</i> sp.			1,L	
LIMIDAE				
<i>Lima</i> sp.		1,S	1,S	
<i>Lima albicoma</i> Dall		1,S		
<i>Lima caribaea</i> Orbigny	S	S	1,S	+
<i>Lima scabra</i> (Born)		S		
LUCINIDAE				
<i>Linga sombreroensis</i> (Dall)	S	F	F	
<i>Lucina radians</i> (Conrad)	S	S	S	
Lucinidae sp. A		S		
Lucinidae sp. B	F			1,S
<i>Myrtea pristiphora</i> Dall & Simpson			1,L	
CHAMIDAE				
<i>Chama lactuca</i> Dall	S	L	1,L	

Table 4 (Continued)

Species	Presence at			Evidence of predation by boring (+)
	125 m	175 m	225 m	
ERYCINIDAE				
<i>Erycina</i> sp.	S			
ASTARTIDAE				
<i>Astarte liogona</i> Dall			1,S	
<i>Astarte smithii</i> Dall			L,1.42*	+
TELLINIDAE				
<i>Tellina persica</i> Dall & Simpson			F	
DREISSENIDAE				
<i>Mytilopsis leucophaeata</i> (Conrad)		S		
VESICOMYIDAE				
<i>Vesicomya</i> sp.		F	S	+
<i>Vesicomya vesica</i> (Dall)	Table1	Table2	L	+
GLOSSIDAE				
<i>Meiocardia agassizii</i> Dall	F	L	F	
VENERIDAE				
<i>Circomphalus callimorphus</i> (Dall)	S	L	F	+
CORBULIDAE				
<i>Corbula caribae</i> Orbigny	1,S			
THRACIIDAE				
<i>Bushia elegans</i> (Dall)	S			
POROMYIDAE				
<i>Cetoconcha</i> sp.		L		
<i>Poromya rostrata</i> Rehder			L	
VERTICORDIIDAE				
<i>Verticordia acuticostata</i> Philippi			F	
<i>Verticordia fischeriana</i> Dall	F		F	
CUSPIDARIIDAE				
<i>Cuspidaria</i> sp.			S	
<i>Cuspidaria microrrhina</i> Dall	L			
<i>Plectodon granulatus</i> (Dall)		L		



Two new Deep-Water *Conus* Species from Barbados, West Indies

BY

FINN SANDER

Bellairs Research Institute, St. James, Barbados, West Indies

(2 Plates)

PROBLEMS INHERENT in collecting of deep-water mollusks dictate that a considerable number of potentially valid species, subspecies and varieties of Conidae remain undescribed. In this connection, shelf-slope margins of islands and continents in tropical regions afford the greatest opportunity for discovering new taxonomic categories of cone shells. It is not surprising, therefore, that notwithstanding previous collections by DALL (1889) and LEWIS (1965) near Barbados, a number of new species of Conidae have been obtained from recent deep-water dredgings off the west coast of the island. Two of these, *Conus hunti* and *C. sanderi*, have been described by WILS & MOOLENBEEK (1979); another two are illustrated and discussed herein.

Conus sorenseni Sander, spec. nov.

(Figures 1 and 2)

Holotype description: Shell is moderately heavy, small (length, 34.5 mm; width, 17.5 mm) and rather slender. Body whorl is straight, but distinctly convex towards the shoulder; surface shiny and smooth except for 14 weakly defined spiral grooves at the base; shoulder roundly angulate; aperture straight and narrow. Spire has 8 postnuclear whorls; protoconch eroded; earliest 2-3 postnuclear whorls appear nodulose; postnuclear whorls have 4-5 striae; lower part of spire convex. Base colour is white with faint pink bands decorated with isolated brown blotches which are more accentuated on the upper band; posterior section of body whorl has faint brown zigzag streaks in continuation with darker markings of same colour on spire whorls.

Paratypes: All sub-adults; respective lengths of paratypes 1, 2 and 3: 16.7 mm, 21.6 mm and 24.7 mm; body whorl as in adult, but may be weakly grooved throughout; shoulder angulate; convexity of holotype spire not apparent and may suggest variability in adults; 2½ shiny, translucent, pale brown nuclear whorls; earliest 2 or 3 whorls weakly nodulose; later whorls with 4-5 striae; base colour white

tinged with pale purple or pink; strength of bands and blotches variable.

Type locality: Off St. James, west coast of Barbados, West Indies, approx. 175 m.

Remarks: Although *Conus sorenseni* is superficially similar to both *C. sanderi* and *C. hunti*, it differs mainly in being larger and relatively heavier. The ground colour in the adult is white contrasted to yellowish-orange and light purple for *C. sanderi* and *C. hunti* respectively. Unlike both *C. centurio* Born, 1778, which lack spiral striae, and *C. ampliurgus* Dall, 1889, which sometimes have indistinct spiral ridges, *C. sorenseni* have pronounced spiral striae. *Conus attenuatus* Reeve, 1844, also collected at the same site, is smaller and more slender. *Conus villeginii* Fischer & Bernardi, 1857, is larger than *C. sorenseni* and, unlike the latter, is moderately light in weight with numerous weak spiral and axial threads over body whorl. Shoulder in *C. daucus* Hwass, 1792, is broader, angulate to carinate, and slightly concave above; body colour never white.

Conus sorenseni appears to be a very rare cone shell, the holotype being the only adult discovered so far.

Deposition of type material: The holotype and paratype 3 are in the collection of the Zoological Museum, Copenhagen; paratypes 1 and 2 are in the respective collections of the author and Mr. Ole Sørensen.

Etymology: *Conus sorenseni* has been named after my good friend and fellow conchologist, Mr. Ole Sørensen of Rancho Santa Fe, California.

Conus knudseni Sander, spec. nov.

(Figures 3 and 4)

Holotype description: Shell is light in weight, small (length, 23 mm; width, 10.9 mm) and slender. Body whorl is almost entirely straight, only slightly convex towards shoulder;

surface shiny and smooth with indistinct spiral grooves on basal third; shoulder angulate; aperture straight and narrow; outer lip thin. High concave spire has 9 postnuclear whorls and protoconch with 2½ shiny, white nuclear whorls; the first 4 post-nuclear whorls with nodulose margins; postnuclear whorls without striae. Main colour is white with two pale orange spiral bands; the base is also weakly coloured; spire whorls marked by faint orange blotches.

Paratypes: Paratype 1, sub-adult (length, 16.8mm; width, 7.4mm); paratype 2, adult (length, 22.8mm; width, 10.7mm). Colour intensity and pattern of paratype 1 is similar to holotype. Shell anatomy of paratype 2 is identical to holotype, but colour markings are more pronounced and bands more variable.

Type locality: Off St. James, west coast of Barbados, West Indies, approx. 175m.

Remarks: *Conus knudseni* is very distinct in shape, spire sculpture, and what can be seen of the pattern (the fresh-dead appearance of all three shells suggests that the "bleached" colouration of two of these is a natural variation). Interestingly, live specimens of *C. mindanus* Hwass, 1792, were collected at the same site with both normal colouration and weakly toned (whitish) shells as in *C. knudseni*. *Conus mindanus* was easily distinguished from the latter by its larger size, relatively heavier shell and distinctly convex sides of the body whorl. *Conus jaspideus* Gmelin, 1791, is more solid, typically has conspicuous spiral ridges on anterior or entire length of body whorl, and lacks pronounced concave spire of *C. knudseni*; *C.*

sanderi Wils & Moolenbeek, 1979, *C. huntii* Wils & Moolenbeek, 1979, and *C. sorenseni* all differ from *C. knudseni* in having prominent striae on the spiral whorls. *Conus attenuatus*, by contrast, is low conical with very elongate body whorl and low to moderately low spire. The prominent protoconch, carinate shoulder and distinct concave tops of the spiral whorls also distinguish this species from *C. knudseni*.

Like *Conus sorenseni*, this is a very rare, albeit unspectacular, cone (only three specimens were collected). Further collections are required not only to describe the radula, operculum and soft parts of the living animals, but also to ascertain the extent of variation in the anatomy of the adult shells of the two *Conus* species.

Deposition of material: The holotype and paratype 1 are in the collection of the Zoological Museum, Copenhagen; paratype 2 is in the author's collection.

Etymology: This new taxon honors my good friend and fellow conchologist, Dr. Jørgen Knudsen, Zoological Museum, Copenhagen.

Literature Cited

- DALL, WILLIAM HEALEY
1889. Report on the Mollusca. Pt. 11, Gastropoda and Scaphopoda, Blake Report, Bull. Mus. comp. Zool. Harv., 18: 1-492
- LEWIS, J. B.
1965. A preliminary description of some marine benthic communities from Barbados, West Indies. Can. J. Zool., 43: 1049-1074

Explanation of Figures 1 to 4

Figure 1: *Conus sorenseni* Sander, spec. nov.; 1, 2 and 3 denote paratypes no. 1, 2 and 3, respectively; 4, holotype.

Figure 2: *Conus sorenseni* Sander, spec. nov.; 1, 2 and 3 denote paratypes no. 1, 2 and 3, respectively; 4, holotype.

Figure 3: *Conus knudseni* Sander, spec. nov.; 1 and 2 denote paratypes no. 1 and 2, respectively; 3, holotype.

Figure 4: *Conus knudseni* Sander, spec. nov.; 1 and 2 denote paratypes no. 1 and 2, respectively; 3, holotype.

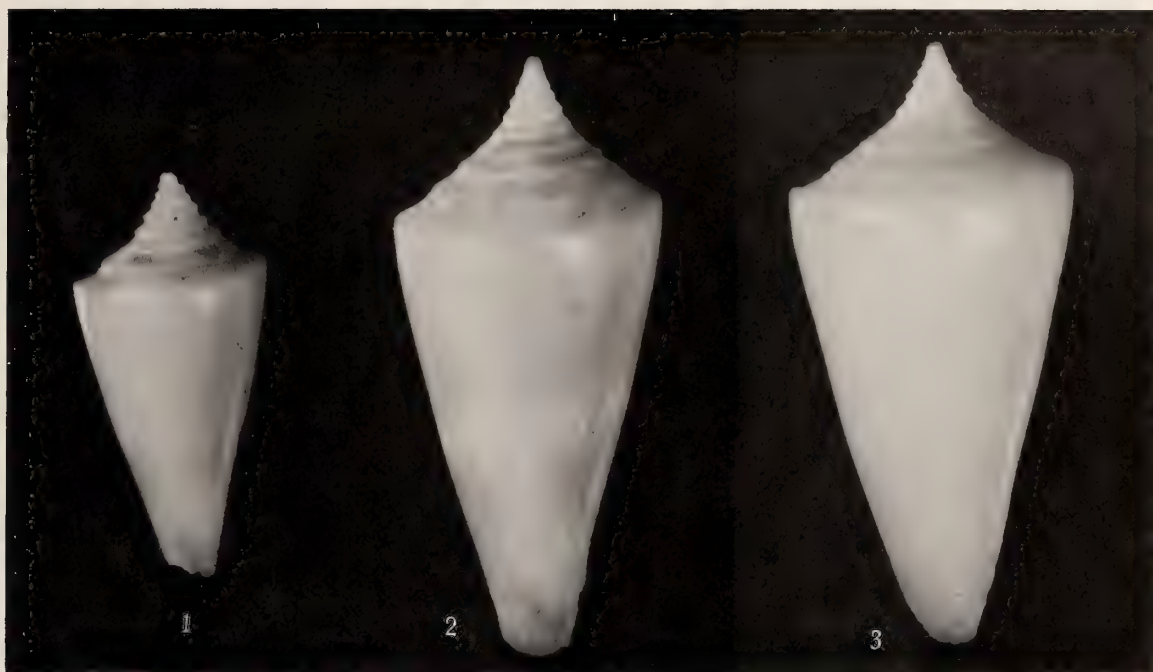


Figure 1

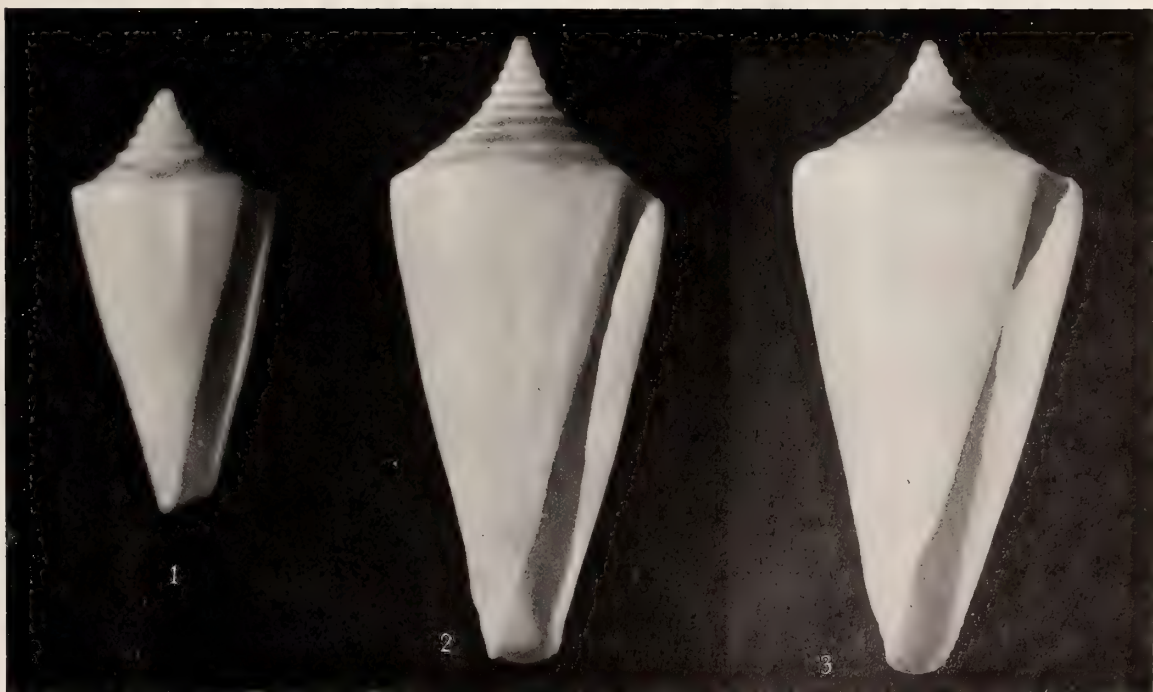


Figure 2

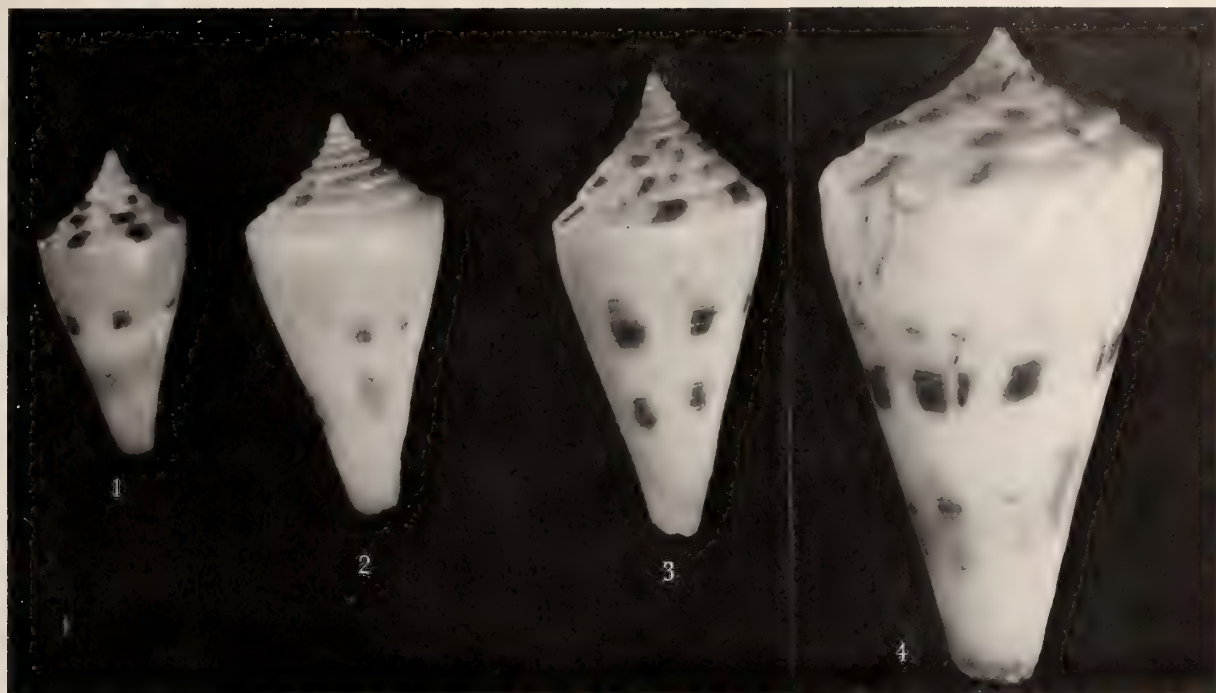


Figure 3

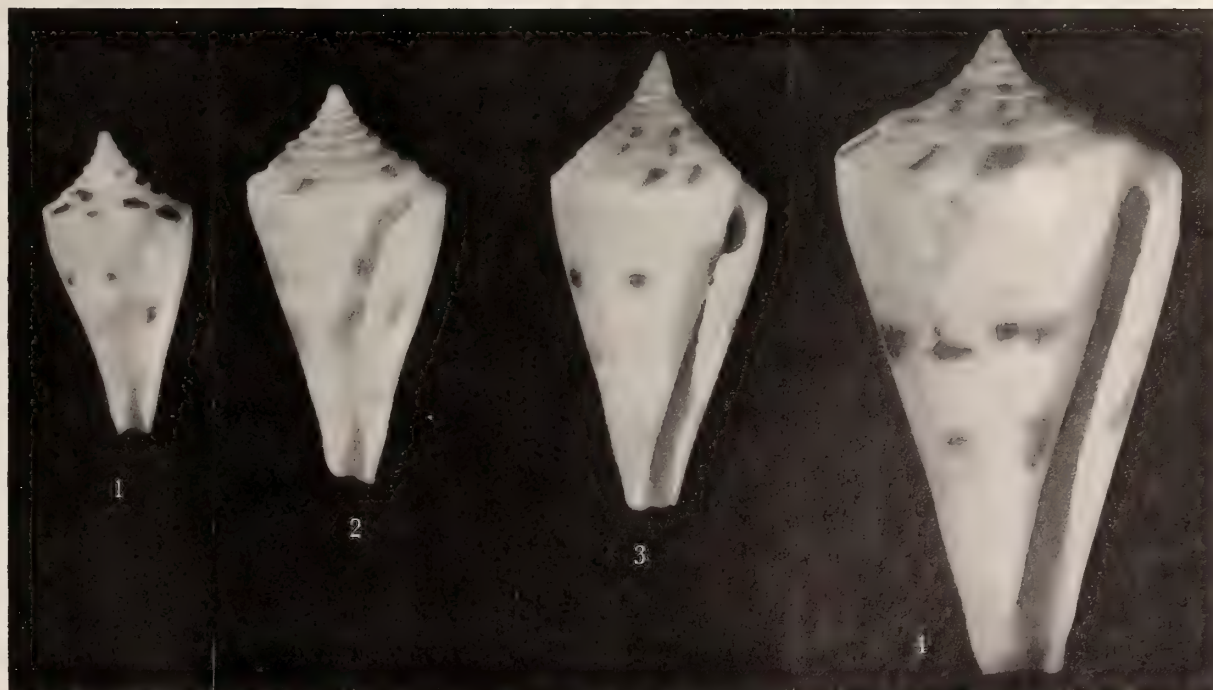


Figure 4

A New Species of *Calloplax*

(Mollusca : Polyplacophora)

in the Eastern Pacific

BY

ANTONIO J. FERREIRA

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(1 Plate; 3 Text figures)

IN A RECENT REVIEW of the genus *Calloplax* THIELE, 1909, in the Americas (FERREIRA, 1978), three species were recognized, *C. janeirensis* (Gray, 1828) in the tropical Caribbean, *C. vivipara* (Plate, 1899) in the warm-temperate region of Chile, and *C. duncana* (Dall, 1919) in the Galápagos Islands. Based upon material in the repositories of the California Academy of Sciences (CAS), Los Angeles County Museum of Natural History (LACM), Allan Hancock Foundation (AHF) [at LACM], and in the private collection of Col. George A. Hanselman, San Diego, California, an additional species of *Calloplax* in the tropical eastern Pacific is here described.

Polyplacophora Gray, 1821

Neoloricata Bergenhayn, 1955

ISCHNOCHITONINA Bergenhayn, 1930

CHAETOPLEURIDAE Plate, 1899

Family diagnosis: Tegmental sculpture strongly defined with rows of pustules or nodules often coalesced in riblets radially disposed on end valves and lateral areas of intermediate valves, longitudinally on central areas. Insertion plates with sharp teeth; intermediate valves uni-slit. Eaves solid. Girdle covered with minute, simple scales, sometimes polymorphic, often with glassy spicules or hairy processes interspersed or both. Radula median tooth wide, subquadrangular; major lateral teeth tricuspid or bicuspid.

Calloplax Thiele, 1909

Generic diagnosis: Elongate in shape (length/width ratio

ca. 2/1). End valves and lateral areas of intermediate valves with strong radial ribs or rows of pustules; central areas with longitudinal, often granose riblets. Mucro elevated, central or slightly anterior with convex, steeply sloping postmucro. Girdle with spicules (not hairs) interspersed amidst small, ovoid, close packed, coarsely-striated scales.

Type species: *Chiton janeirensis* Gray, 1828, by M.

Calloplax hanselmani Ferreira, spec. nov.

(Figures 1 to 3, 7, 8, 4 to 6)

Chaetopleura cf. *C. mixta* (Dall, 1919) (SMITH & FERREIRA, 1977: 85-86; figs. 6, 7).

Diagnosis: Small size chitons, dark greenish. Tegmentum with relatively large pustules arranged in radial rows on end-valves and lateral areas. On central areas, longitudinal rows of smaller pustules converging forward. Mucro central or slightly anterior; postmucro area convex. Girdle with polymorphic, mostly ovoid, small, coarsely striated scales and interspersed glassy spicules; girdle bridges empty.

Type Material: Holotype (CAS 017703); Paratypes (CAS 017705; CAS 017706; CAS 017707; CAS 006140).

Type Locality: Academy Bay, Isla Santa Cruz, Galápagos Islands, Ecuador (0° 43' S; 90° 20' W).

Description: Holotype (Figures 1, 2, 3)—Subcarinate; elongate, 6.0mm long, 3.5mm wide (including girdle). Color dark grayish green. Tegmentum pustulose; larger pustules (100-130µm in diameter, up to 150µm in height) disposed in radial rows on anterior valve (about 16 rows), lateral areas of intermediate valves (3-4 rows), and postmucro area of posterior valve (about 10 rows); smaller pustules (about 70µm in diameter, up to 50µm in height) aligned in forward-converging longitudinal rows on central areas

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(about 10 rows per side). Jugum smooth except for some few, low profiled, almost obsolete pustules. Lateral areas markedly elevated, particularly on anterior valves. Posterior edge of valves straight, not beaked. Width of valve i, 2.3mm; of valve viii, 2.2mm. Mucro central, inconspicuous; postmucro area moderately convex. Articulamentum greenish white. Insertion teeth well defined, relatively sharp; slit formula, 8-1-10. Sutural laminae subquadran-gular, particularly on valves iii-vii, semi-ovate on valve viii. Sinus well defined. On valve viii, width of sinus 0.3 mm, width of sutural laminae 1.0mm, ratio (relative width of sinus) 0.30. Eaves solid.

Girdle's upper surface paved with small (about $40 \times 20 \mu\text{m}$), ovoid scales, coarsely striated toward pointed end (Figure 4) and few glassy spicules up to $300 \mu\text{m}$ long inter-

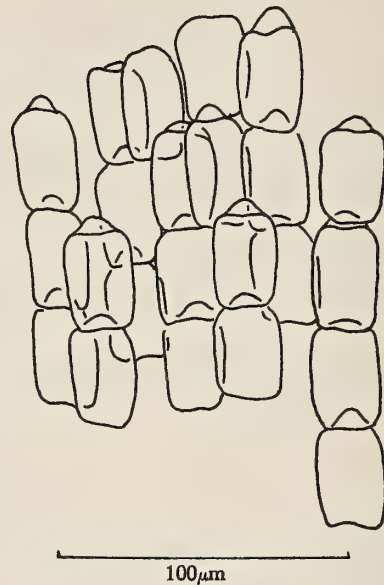


Figure 5

Calloplax hanselmani Ferreira, spec. nov. Holotype. Ventral girdle scales.

spersed. Girdle bridges (Ferreira, in press) empty; i.e., devoid of spicules or other scale-like elements. Undersurface paved with rectangular, transparent scales, about $400 \times 220 \mu\text{m}$, bearing an outer edge protuberance that articulates with adjacent scale's inner edge concavity (Figure 5). Radula, 2.5mm long (42% of specimen's length) with some 35 rows of mature teeth; median tooth, broadly rectangular, about $32 \mu\text{m}$ at anterior blade; major lateral teeth with tricuspid head (Figure 6).

Paratypes: Together with the holotype, ten other specimens of *Calloplax hanselmani*, here designated paratypes, were collected at Academy Bay, Isla Santa Cruz, Galápagos Islands, Ecuador, at four different stations in the intertidal zone by A. G. Smith and Jacqueline De Roy, in 1964-1967. The specimens display very little variation in color, sculpture, and tail valve characteristics, but the number of glassy spicules in the girdle is quite variable. Largest paratype, 9mm long. Slit formula of a paratype 6.4mm long, 8-1-10. A paratype, 6.7mm long (CAS 017707) is figured here (Figure 7); another, 7.3mm long (CAS 017706) was previously illustrated (SMITH & FERREIRA, 1977: figs. 6, 7).

Referred Material:

1) 3 specimens, largest 9.0mm long, Yacht Club beach, Mazatlán, Sinaloa, Mexico ($23^{\circ}13'N$; $106^{\circ}25'W$), leg. Howard & G. Sphon, 1st Churea Expedition, 20-23 Dec. 1961 (CAS 010112).

2) 3 specimens, dry, largest 8.2mm long, Punta Marinero, Mazatlán, Sinaloa, Mexico, leg. G. A. Hanselman, 9 Feb. 1971, intertidal (G. A. Hanselman Colln.) (Figure 8).



Figure 4

Calloplax hanselmani Ferreira, spec. nov. Holotype. Dorsal girdle scales and spicules.

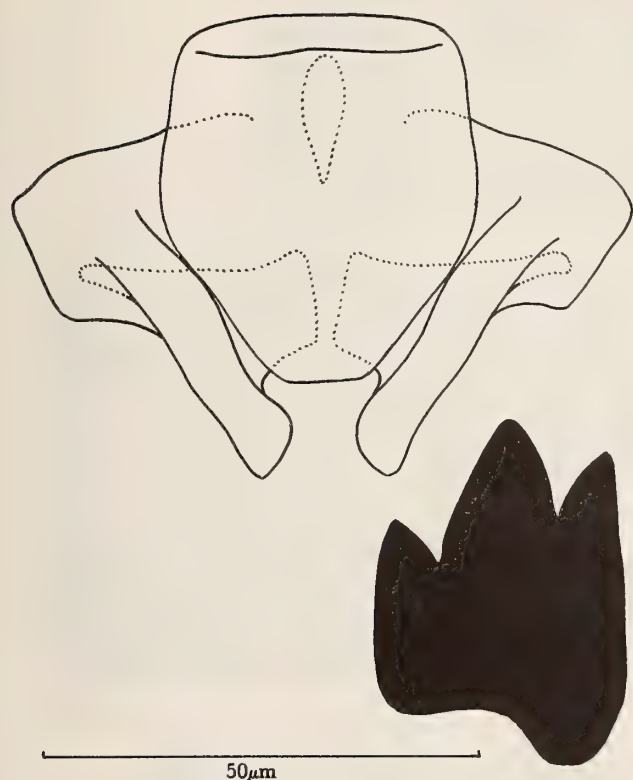


Figure 6

Calloplax hanselmani Ferreira, spec. nov. Holotype. Radula: Median tooth, first lateral teeth, and head of major lateral tooth.

- 3) 1 specimen, in alcohol, 6.6mm long, North Beach, Mazatlán, Sinaloa, Mexico, leg. A. G. Smith, 9 Mar. 1945 (CAS 010114).
- 4) 2 specimens, dry, largest 8.8mm long, Punta Piaxtla, Sinaloa, Mexico, leg. D. Shasky, 24 Dec. 1962, intertidal (CAS 025395).
- 5) 8 specimens, dry, largest 6.8mm long (slit formula 8-1-9), Tangola-Tangola Bay, Oaxaca, Mexico (15°46'N; 96°06'W), leg. L. G. Hertlein, 16 Dec. 1931 (CAS 025396).
- 6) 1 specimen, 11 mm long, in alcohol, off Tumbes, between Caleta La Cruz and Punta Pizano, Tumbes Prov., Peru (3°28'S; 80°36'W) leg. J. H. McLean & D. Shasky, on shrimpboat *Maria Helena*, 13, 14 Apr. 1972 (LACM 72-83).
- 7) 1 specimen, in alcohol, 16.2mm long, Sechura Bay, Peru (5°39'S; 81°01'W), 15 Feb. 1938, at 9.5 fathoms (17.3m), (LACM-AHF 845-38).
- 8) 5 specimens, in alcohol, largest 11.2mm long (slit formula, 9-1-8), Isla Lobos de Afuera, Peru (6°57'S; 80°42'W), leg. J. H. McLean, Jan. 1974 (LACM 74-6).

Distribution: *Calloplax hanselmani* seems to be confined to the tropical eastern Pacific with a geographic range extending between 23° 13' N and 6° 57' S, and bathymetric range from 0 to 17 m.

Individual Variation: Among the 35 specimens of *Calloplax hanselmani* examined (including type material) there was relatively little variation. In color, dark green predominates but a few specimens are brighter brown to cream; one specimen shows white in two of the intermediate valves, another red at the jugum. Larger specimens with more numerous pustules on lateral areas and end valves, and more convex postmucro. Largest specimen examined, 16.2mm long. Slit formulae, 8/9-1-9. No essential differences were found between Galápagos and mainland specimens.

Remarks: The small size of the specimens of *Calloplax hanselmani* collected in the Galápagos Islands suggested at first that they might be juveniles of some unrecognized species in the genus *Chaetopleura* Shuttleworth, 1853 (SMITH & FERREIRA, 1977). The finding of conspecific populations along the coast of Mexico and Peru permitted the recognition of a new species and its assignment to the genus *Calloplax*, instead.

The taxonomic position of *Calloplax* has remained uncertain. Erected by THIELE (1909) to accommodate *Chiton janeirensis* (theretofore assigned to *Chaetopleura*), *Calloplax* was allocated to Chaetopleuridae in early works (THIELE, 1929; BERGENHAYN, 1930; SMITH, 1960), to Callistoplacidae more recently (SMITH & FERREIRA, 1977; VAN BELLE, 1978; FERREIRA, 1978). The question hinges on the assessment of the similarities between *Calloplax* and *Chaetopleura* on the one side and *Callistochiton* on the other. *Calloplax* resembles *Callistochiton* in the 1) elongated shape; 2) general characteristics of the valves with their strong tegmental sculpture of radial ribs on end valves and lateral areas of intermediate valves; 3) correspondence between articulation slits and tegmental ribs; and 4) tendency towards an upswept vii valve. It approaches *Chaetopleura* in the 1) pustulose tegmental sculpture; 2) girdle upper surface elements of relatively undifferentiated small scales interspersed with glassy spicules, and under surface rectangular scales; and 3) radula with wide, sub-quadrangular median tooth and tricuspid major lateral teeth. The relative merits of these similarities indicate that *Calloplax* is phylogenetically closer to *Chaetopleura* than to *Callistochiton* and, therefore, that its allocation to Chaetopleuridae is amply justified.

Integumental sculpture and girdle elements, *C. hanselmani* is definitely distinct from the two other congeneric species in the eastern Pacific, *C. vivipara* and *C. duncana* (see FERREIRA, 1978). However, it bears notable resemblance to the Caribbean *C. janeirensis* particularly in the strongly pustular sculpture of the end valves and lateral areas of the intermediate valves, and in the ovoid, coarsely striated girdle scales. The similarities between *C. hanselmani* and *C. janeirensis* are such as to suggest that the two species might have separated at relatively recent geologic times, perhaps in the Mid-Pliocene at the emergence of the Panamanian barrier. Based on the specimens examined, *C.*

hanselmani is seen to differ from *C. janeirensis* in the 1) much smaller size, 2) less prominent tegmental sculpture, and 3) empty girdle bridges.

The species is here called *hanselmani* after a good friend, Col. George A. Hanselman, San Diego, California, enthusiastic chiton collector, who has made many valuable contributions, both in specimens and ideas, to this and other works.

ACKNOWLEDGEMENTS

For their valuable help in several phases of this work I wish to express my appreciation to Dr. Welton L. Lee, Dustin D. Chivers, Dalene Ried, and Barbara Weitbrecht, Department of Invertebrate Zoology, and Dr. Peter U. Rodda, Department of Geology, California Academy of Sciences; Dr. James H. McLean and Gale Sphon, Natural History Museum of Los Angeles County; Dr. Joseph Rosewater, U.S. National Museum of Natural History; Col. George A. Hanselman, San Diego, California; and Laura B. Shy, Westminster, California. Credit for the drawings is due to Barbara Weitbrecht.

I am particularly grateful to Dr. Barry Roth, Department of Invertebrate Zoology, California Academy of Sciences for attentive advice and critical readings of the manuscript.

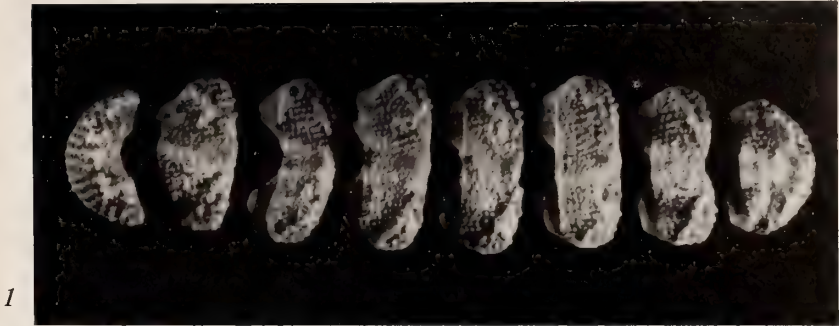
Finally, with pride, I want to acknowledge the influence upon my work of my son, Carl J. Ferreira, who introduced me to and taught me how to use a computer.

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Explanation of Figures 1 to 3 and 7, 8

- Figure 1: *Calloplax hanselmani* Ferreira, spec. nov. **Holotype**. Disarticulated valves.
- Figure 2: *Calloplax hanselmani* Ferreira, spec. nov. **Holotype**. Tegmental surface of valves i, iv, and viii.
- Figure 3: *Calloplax hanselmani* Ferreira, spec. nov. **Holotype**. Articulament surface of valves i, iv, and viii.
- Figure 7: *Calloplax hanselmani* Ferreira, spec. nov. **Paratype**, 6.7 mm long (CAS 017707).
- Figure 8: *Calloplax hanselmani* Ferreira, spec. nov. Specimens 8.2, 7.2 and 5.2 mm long, collected at Punta Marinero, Mazatlán, Sinaloa, Mexico (G. A. Hanselman Colln.).



Observations on the Ultrastructure and Defensive Behavior of the Cnidosac of *Cratena pilata*¹

BY

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(3 Plates)

INTRODUCTION

Chrysaora quinquecirrha DeSor, the sea nettle, is a venomous jellyfish commonly found in the Chesapeake Bay. Recent investigations here revealed several different nematocysts on the medusal fishing tentacles but only one fully formed stage on the polyps (BURNETT *et al.*, 1968; SUTTON & BURNETT, 1971). The aeolid nudibranch, *Cratena pilata* (Gould, 1870) is an active predator upon the various semaeostomes in the Chesapeake Bay (CARGO & SCHULTZ, 1967). It feeds eagerly on all nematocyst-bearing tissues of these jellyfish but appears to prefer the scyphistoma or polyp stage.

Earlier investigators have shown that aeolids ingest and store undischarged jellyfish nematocysts in a sac-like organ (cnidosac) located near the terminus of the cerata for defense. KEPNER (1943) detailed the means by which *Aeolia (Cratena) pilata* ingested the nematocysts of a common hydrozoan, *Pennaria tiarella* (Ayres, 1852). He observed that only the penetrant nematocyst types, in this case the microbasic mastigophores were transferred intact to the cnidosacs at the tips of the cerata while the volvent (entangling) and other less virulent or irritating types were digested.

Nematocyst appropriations by sea slugs was also reviewed by EDMUNDS (1966), GROSVENOR, (1903), MARISCAL (1974) and by THOMPSON & BENNETT (1969, 1970). The latter investigators reported that the nematocysts of the normal prey of glaucid nudibranchs; *i.e.*, hydrozoans and pelagic

cnidarians such as *Velella* Lamarck, 1801 and *Porpita* Lamarck, 1801 were not often found in the cnidosacs while the largest, more potent *Physalia* nematocysts were.

The nudibranch discussed here was originally identified as *Coryphella* sp. and then as *Cratena pilata*. The taxonomic identity has been the object of some doubt and conjecture for a number of years. Despite some recent unpublished work (VOGEL, 1977) listing *C. kaoruae*, Marcus, 1957, as a synonym, we are employing *C. pilata* and cite MARCUS (1972) as the latest published authority.

As part of the overall sea nettle investigations being pursued in Maryland, certain observations were made to elucidate the structure of the *Cratena* cnidosac and to more fully understand how this aeolid employs these stinging cells for its own defense.

Materials and Methods

Polyps of *Chrysaora quinquecirrha* were fed to *Cratena pilata* for several days prior to sacrifice of the mollusc. The cerata of these animals were removed and prepared for examination as described below. Cerata of the same animals were also used to verify the stinging potential by pressing them against the mucosal surfaces of the lips of human volunteers.

Cerata of adult *Cratena pilata* were removed with forceps and placed in river water (Patuxent River, Md.; salinity = 18‰) on a depression slide for direct microscopic examination. Similar specimens were anesthetized with 5‰ chloral hydrate and preserved in 2‰ formalin in river

¹ Contribution No. 1228, Center for Environmental and Estuarine Studies of the University of Maryland.

water. This tissue was embedded in 1.3% agar and stained with phosphotungstic acid-hematoxylin reagent and sectioned.

Other cerata were fixed in 6% glutaraldehyde in river water and prepared for electron microscopy according to previously described techniques (SUTTON & BURNETT, 1969).

The circuit of a 6-volt lantern battery was completed in river water across a 2.5 cm space on a depression slide to assess the effect of electric current on the ceras.

RESULTS

1. Structure of the cnidosac and the distal wall of ceras.

The cerata are finger-like projections (Figure 1) on the dorsal surface of the aeolid. Most of the central core of the ceras is occupied by liver tissue. Near the tip and partially pressed to one side of the liver tissue is the cnidosac containing nematocysts. This structure opens to the outside of the ceras terminus by an indistinct pore (Figure 2).

The cnidosac is an inner cavity surrounded by two circular walls. Varying sizes of only one form of intact nematocysts were present inside the cavity (Figure 3). These organelles are composed of a multilaminated capsule enclosing a central thread. The thread is composed of a proximal, dilated butt and many coils of the tapering distal portion. The matrix of the capsule is electron-dense and homogeneous in the periphery but is broken up into clumps in the center. The nematocysts thus enclosed are separated from each other by a network of trabeculae. In some instances cellular debris is adherent to the outside of the nematocyst capsule (Figure 3).

The inner surface of the cnidosac wall is lined with a unit membrane. Large vacuolated cells lie on this membrane (Figure 4). A layer of elongated cells containing multidirectional muscle fibers covers these cells. These

muscle cells are, in turn, surrounded by another thin layer of vacuolated cells (Figures 4 and 5). The outer wall of the ceras is multilayered and lies upon the muscle fibers (Figure 6). This layer contains multiple tiers of oval vacuolated cells with large granular nuclei and a granular cytoplasm. The exterior border of these cells is lined with cilia. Mucous gland cells are located at any level within these tiers.

2. Studies on the release of nematocysts from the ceras.

All batches of cerata used in these experiments were capable of producing pain when contacting human mucosa. The nematocysts were tightly packed within the sac of living cerata. When a 6-volt DC current was applied, the ceras recoiled from the positive terminal and occasionally caused the cnidosac to express a portion of its contents. Very few of the ejected nematocysts fired their threads under this electrical stimulus (Figure 7).

The addition of a drop of 5% formalin to the depression slide containing a ceras, however, invariably caused the cnidosac to partially discharge its contents. Almost all the nematocysts discharged in this manner by formalin fired their threads and were released from the cnidosac in spherical bunches of 25-50 nematocysts. About 25 bunches constituted a release (Figure 7). A single ceras can repeat this act at least once and still retain some nematocysts.

DISCUSSION

Cratena pilata (and presumably other related species) derive diverse advantages from the presence of numerous cerata on the dorsal surface. Although they are principally a digestive and respiratory apparatus, there is little doubt of their defensive ability. When touched or irritated, the slug invariably responds by bristling its cerata and curling its

Explanation of Figures 1, 2 and 7

Figure 1: Side view of *Cratena pilata* (life size = 22 mm long) (Courtesy of M. J. Reber)

Figure 2: Cross section of *C. pilata* ceras at level of cnidosac. × 560

Figure 7: Tip of ceras after a cnidosac discharge. Note the nematocysts remaining inside the sac as well as the group being everted. × 530

Explanation of Figures 3 and 4

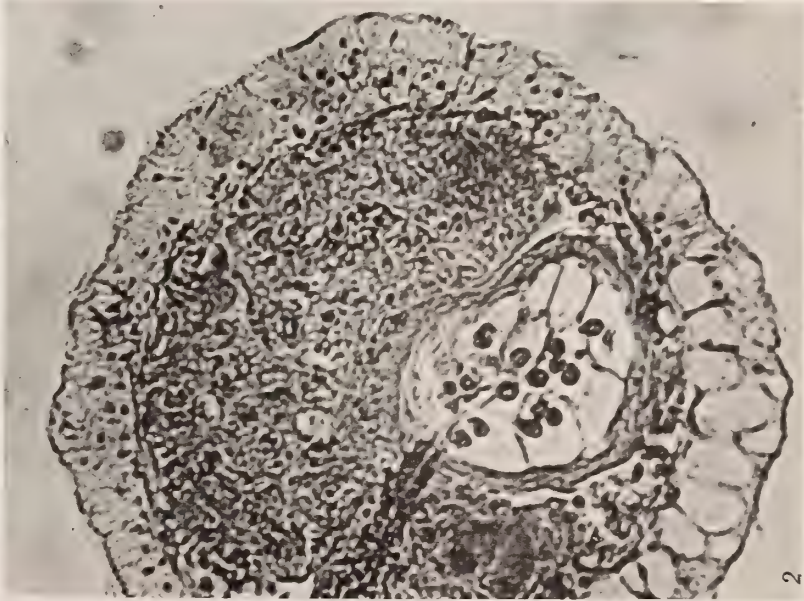
Figure 3: Ultramicroscopic cross section of sea nettle nematocysts within cnidosac × 3720

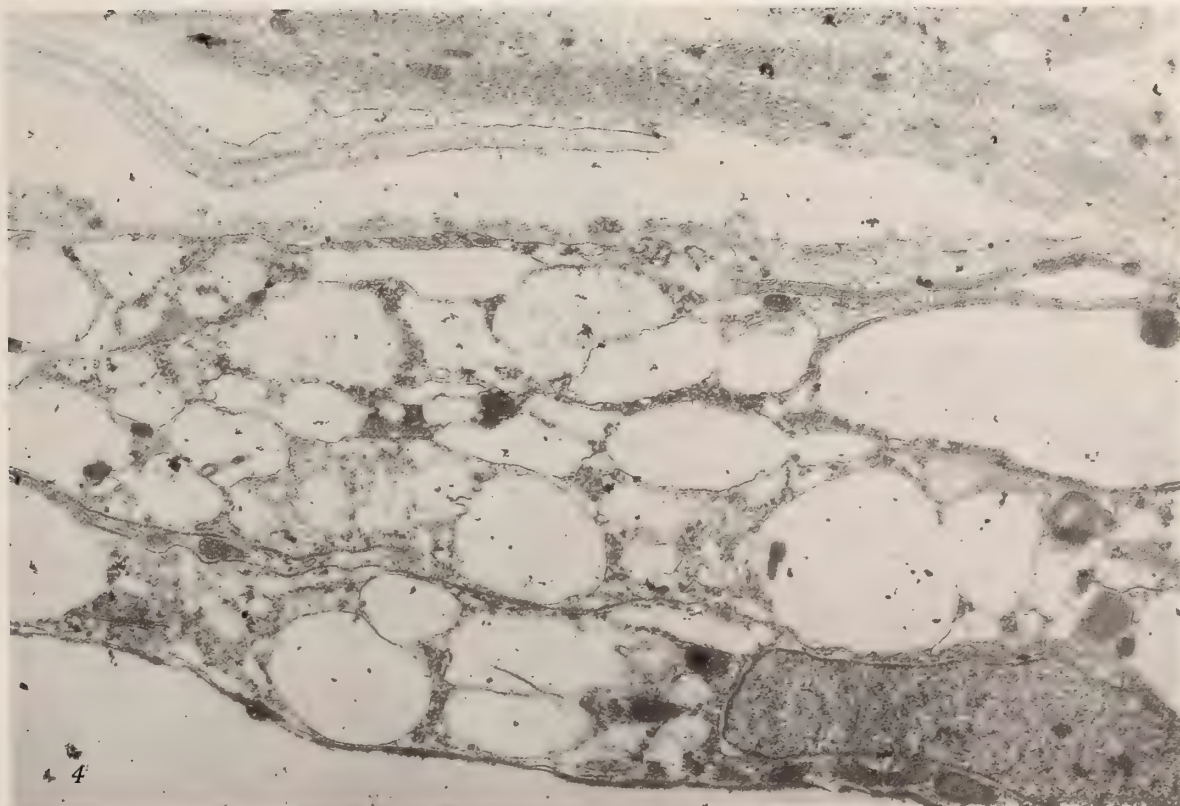
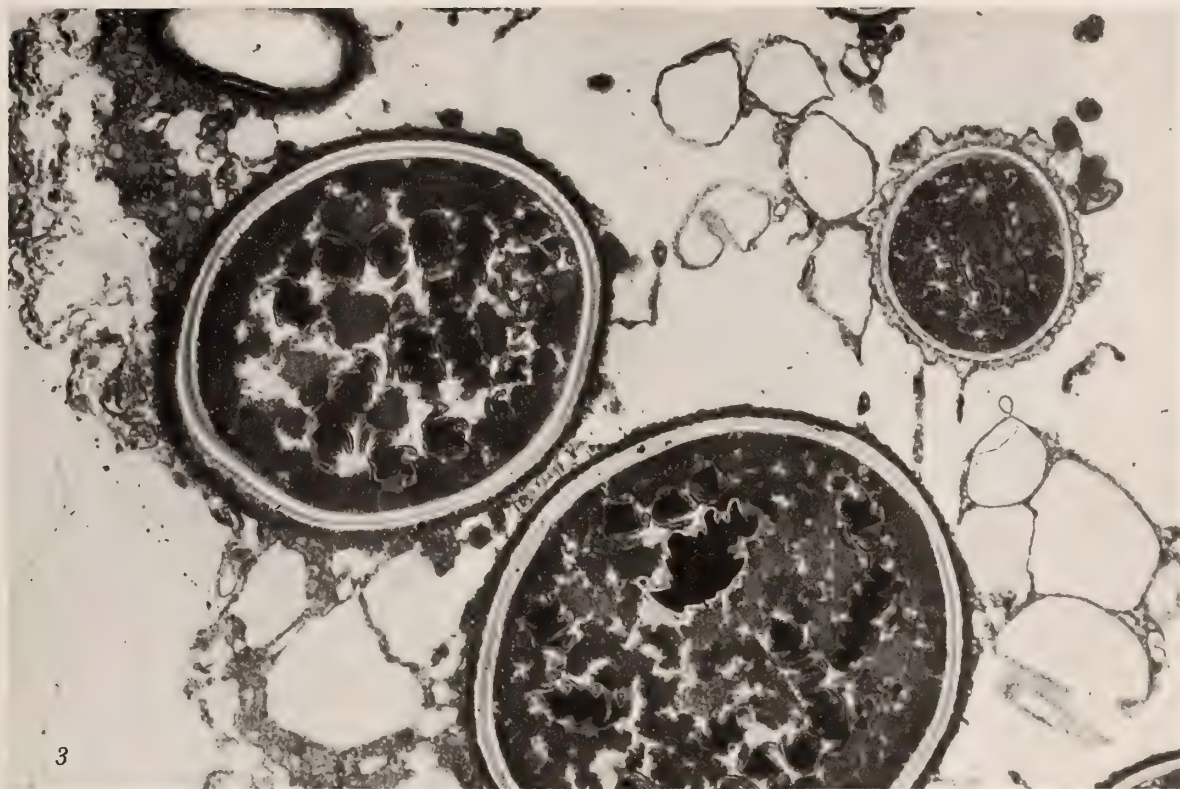
Figure 4: Ultramicroscopic view of wall of cnidosac and inner surface of ceras × 4500

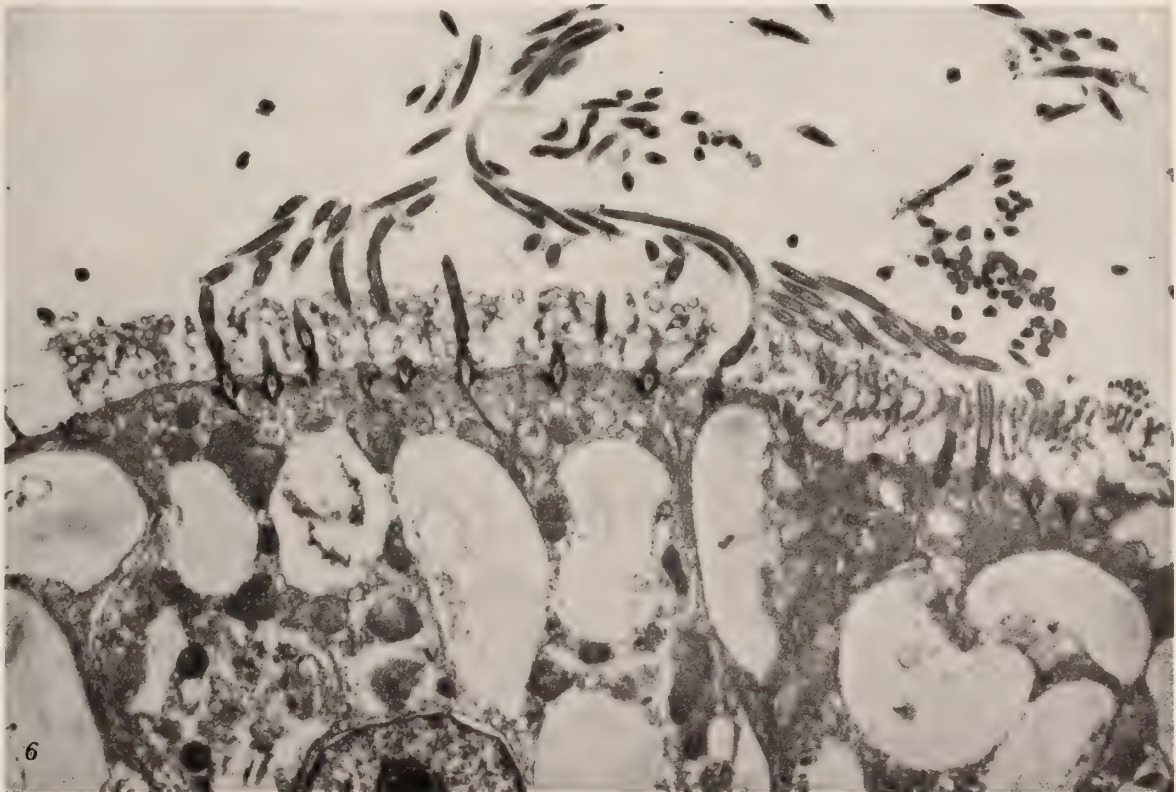
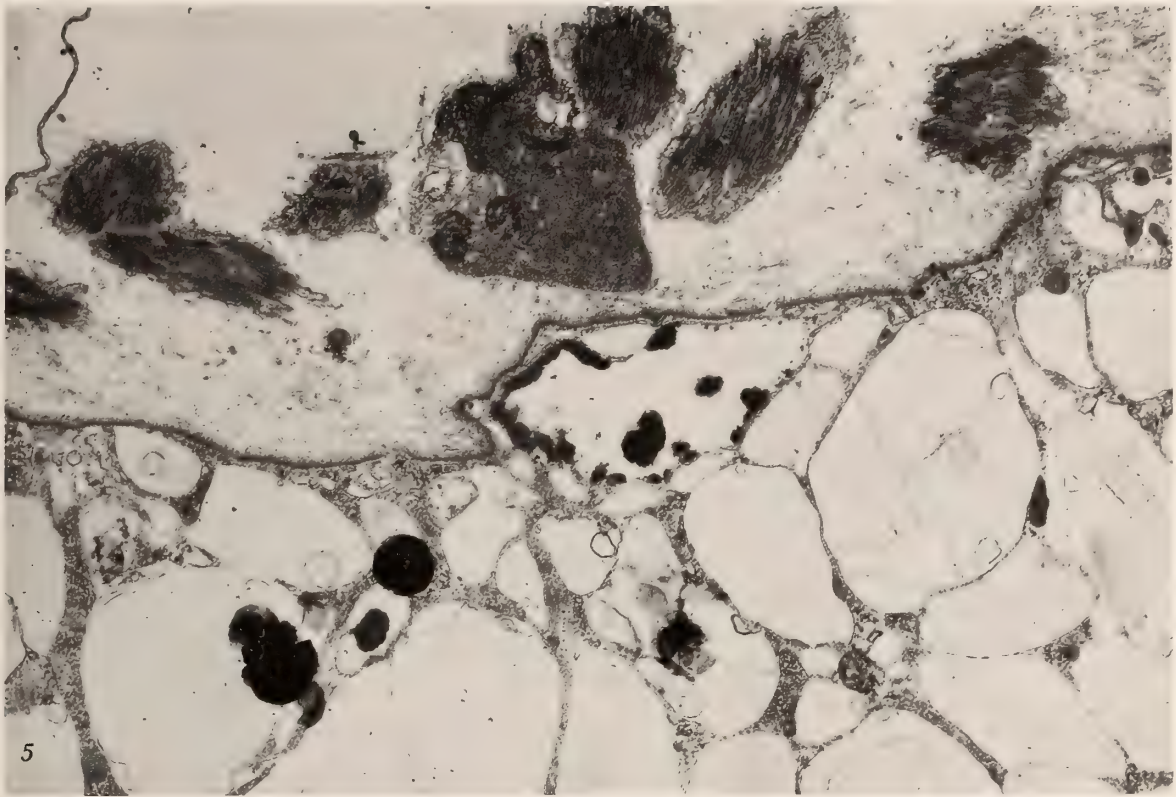
Explanation of Figures 5 and 6

Figure 5: Ultramicroscopic view of the wall of ceras-junction of muscle tissue and outer vacuolated cell layer × 3200

Figure 6: Ultramicroscopic view of outer layer of ceras wall showing ciliary border × 4050







body ventrally, thus making it difficult for a predator to avoid the cerata with their stinging cell-bearing sacs.

Several unusual features of the cnidosac discharge were noted:

1. The organelles were released in bunches, rather than individually. Such a release pattern which appears to be efficient defensively might be a direct result of a deliberate storage pattern within the sac.
2. Each release only partially emptied the cnidosac thus allowing a second discharge. This behavior allows the aeolid to maintain a defensive capacity even though it hasn't ingested additional toxic nematocysts.
3. Chemical rather than electrical stimuli caused a complete eruption of the ceras plus discharge of the extruded nematocysts. These results suggest that the mollusc has two separate defensive processes, cerata eruption and nematocyst discharge.

We mentioned earlier that several investigators have added to the understanding of the slug's ability to ingest and physiologically sort and subsequently concentrate only virulent, penetrating types of hydrozoan nematocysts. In so doing, the slug acts like a biological filter, selecting and sorting only venomous nematocysts. A similar response is reported here. Although the *Chrysaora* polyps possess only one fully developed type of nematocyst, a heterotrichous microbasic eurytele, the cnidosac of a well fed *Cratena pilata* is completely filled with these highly toxic and irritating cnidae. There was no evidence of other food particles within the cnidosac even though the digestive diverticula leading to them contained a variety of partially digested food particles.

We have not attempted to identify all of the structures present within and upon the cerata. The outer epithelium is covered with cilia, which presumably keep the surface clean and maintain a moving current of water upon it (Figure 6). The multidirectional muscle layer of the ceras wall is larger than that of the cnidosac. Its function is constant and varied while the sac is only required to spasmodically contract on infrequent occasions. Many vacuolated cells, especially on the inner wall of the ceras were noted. These structures may be old mucus cells since many nascent and mature mucus-producing cells were observed in this region.

This study has defined several anatomical and behavioristic aspects of ceras development in *Cratena pilata*. This species is found over a wide geographic range and feeds on a variety of cnidarian prey. However, in the Chesapeake Bay where sea nettle scyphistomae are abundant, it

appears to prefer this organism, feeding on it avidly and transferring large numbers of toxic and irritating nematocysts to the tips of its cerata. It then has the capability to discharge as many as 500 nematocysts from each of its cerata and perhaps repeat this defensive action once. A slug 12mm long bears about 45 cerata (VOGEL, 1977). From these observations, it is obvious that this mollusc derives a potent deterrent to predation from its association with a noxious coelenterate.

ACKNOWLEDGMENTS

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Notes on the Fine Structure of the Head-Wart in Some Terrestrial Snails

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(3 Plates; 1 Text figure)

INTRODUCTION

THE DORSAL SURFACE of the snail is covered with numerous ordinary polygonal tubercles. The head-wart is a tissue between the optic tentacles in some terrestrial snails (TAKI, 1935), composed of modified dermal tubercles. In the breeding season, the snails become quite sensitive and their head-wart forms a conspicuous hemispherical protrusion. The swelling of the head-wart and mating behavior occur at the same time. The head-wart has been demonstrated to be a sex pheromone-secreting gland (TAKEDA & TSURUOKA, 1979). The head-wart cells are characterized by the drastic elongation of the epithelial cells from cuboidal to columnar. Recently, its development has been demonstrated to be controlled by the gonadal factor, testosterone, secreted from the hermaphrodite gland (TAKEDA, 1980a). The fine structure of the head-wart has not been studied. The present note mainly reports the fine structure of the head-wart through scanning electron microscopy as well as ordinary electron microscopy.

MATERIALS AND METHODS

Materials used in the observations were some terrestrial snails such as *Euhadra*, *Bradybaena*, *Satsuma*, *Chlorites*, *Aegista*, *Dolicheulota*, *Trishoplita* and *Helicostyla*, commonly living in Japan.

For scanning electron microscopy, glutaraldehyde and osmium tetroxide-fixed head-warts were dehydrated in gradual concentrations of ethanol and acetone and were dried by the critical point method, using liquid CO₂. They were then coated in a vacuum evaporator and LB-1 in cleanor. Scanning electron micrographs were taken with JSM-1 with an accelerating voltage of 10 k.v.

For ordinary electron microscopy, the head-warts were fixed in buffered 3% glutaraldehyde with 0.1 M phosphate buffer, at pH 7.4 for 1 hour and the post-fixed in buffered

1% osmium tetroxide with 0.1 M phosphate buffer, at pH 7.4 for 2 hours. They were then dehydrated in gradual concentrations of ethanol and acetone and embedded in Epon 815. Thin sections were cut on an LKB ultratome and stained with lead-citrate. They were examined with a JEM 100B electron microscope.

RESULTS

There are three types of head-warts. The first type is a crescentic depression, called a "head hollow" by TAKI (1935); it occurs in *Satsuma* and *Chlorites* (Figure 1 A, a and b). The second type, S-shaped tubercles, appeared in *Aegista* and *Trishoplita* (Figure 1 B, a and b). The third type consists of a row or small mass of warty tubercles and occurs in *Euhadra*, *Bradybaena* (Figure 1 C, a and b), *Dolicheulota*, and *Helicostyla*. The head-wart of the third type was far more conspicuous than the other two.

The surface fine structure of the head-wart in the adult snail *Euhadra peliomphala* is shown in Figures 2 and 3. The tip of the columnar epithelium formed a tuft-like structure (Figure 2). The crossed lateral view is shown in Figure 3. The columnar epithelial cells are arranged side by side on the connective tissue. Similar structures were also found in the other snails examined.

The general fine structure of the head-wart cells in the adult snail *Euhadra peliomphala* is shown in Figure 4. The free surface of the cells was a microvilli structure. Particles were often attached to the microvilli. Occasionally, protrusions were seen at the tip of it. They can bud off, similar to apocrine secretion. Beneath the microvilli lay a very distinct terminal web containing many microfilaments (Figure 5). Adjacent epidermal cells were held together by interdigitation (Figures 4, 5 and 6). They were closely appressed to each other, particularly in the apical half of the cells. The most apical junction where external surface membranes meet, formed the zonula adherens. Below it,

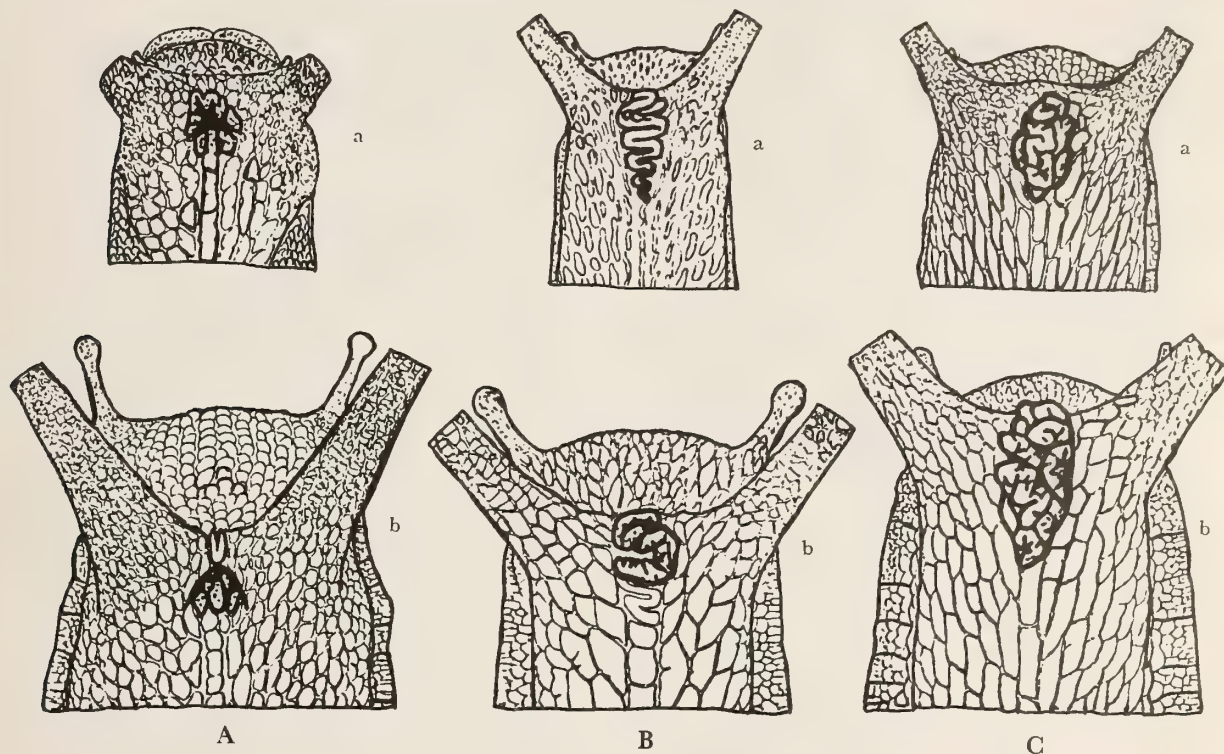


Figure 1

Three types of the head-wart in dorsal view

- A: The head-warts in (a) *Chlorites* and in (b) *Satsuma*
 (B): The head-warts in (a) *Trishoplita* and in (b) *Aegista*
 (C): The head-warts in (a) *Bradybaena* and in (b) *Euhadra*

septate junctions were present. As to cell organelles, mitochondria and free ribosomes were numerous. A granular endoplasmic reticulum was typical. The development of a smooth endoplasmic reticulum was not evident. Near the Golgi apparatus, some large granules were present. In the breeding season, the Golgi apparatus developed well and many granules were usually found near its area (Figure 6). These granules seem to be synthesized by the Golgi apparatus and to concern the sex pheromone. There exist goblet cells between ordinary and warty epithelial cells (Figure 5). These structures were also found in the other snails examined.

DISCUSSION

Specialized dermal structures are classified in three types on the vertex in the region between large tentacles in some pulmonates. These are the "Cephalic dimple" of *Achatina achatina* (see CHASE & PIOTTE, 1981), the "Frontal organ" of *Gymnarion* (BINDER, 1965) and the "Head-wart" in Camaenidae such as *Satsuma* and *Chlorites*, and Bradybaenidae such as *Helicostyla*, *Aegista*, *Bradybaena*, *Euhadra*, *Dolicheulata* and *Trishoplita* (TAKI, 1935, TAKEDA & TSURUOKA, 1979). The head dimple is a form of a depression of the skin surface. The frontal organ is situated above the snail's mouth,

between four tentacles and usually rather nearer the dorsal pair. Furthermore, the "Fossette triangulaire caudale" (ANDRÉ, 1898) or the "Caudal gland" (BARR, 1928) of the slug, *Arion*, occurs in the dorsal mid-line and has some similarity to the head dimple. These dermal structures are not pathological but normal structures, and have some specific function, except the head-wart of *Rumina decollata* (see MILES 1961).

All these structures have been known to have some functions in courtship behavior in *Euhadra* (TAKEDA & TSURUOKA, 1979; TAKI, 1935; YAMADA, 1962), *Gymnarion* (BINDER, 1977), *Achatina* (CHASE & PIOTTE, 1981) and other species (TAKI, 1935; YAMADA, 1962). In *Euhadra peliomphala*, castration led to the atrophy of the head-wart, and subsequent injection of hermaphrodite gland homogenate induced the development of the head-wart (TAKEDA, 1980a). Furthermore, the snail's gonad synthesized the sex steroids such as testosterone and estradiol, like vertebrates, and these steroids play an important role in reproduction in pulmonates (TAKEDA, 1979; 1980a; 1980b). By organ culture methods, the head-wart in *Euhadra* has been demonstrated to be the target organ of testosterone (TAKEDA, 1980a). Other reproductive accessory sex organs have also been shown to be controlled by the steroid hormones secreted from the hermaphrodite gland (TAKEDA & TAKAYANAGI, 1979; 1980; TAKEDA & NOMIZO, 1980; TAKEDA, TSUKAMOTO & YAMAMOTO, 1980; TAKEDA, ABE & TANAKA, 1981).

On the ultrastructure of the molluscan epidermis, very little research has been performed. The cell junctions in the head-wart are similar to those found in the epidermis in the snails *Lymnaea stagnalis*, *Biomphalaria pfeifferi*, and *Helix pomatia* (ZYLSTRA, 1972) and the slugs *Arion rufus* and *Arion empiricorum* (see WONDRAK, 1967; 1968). The interdigitation developed more in the terrestrial pulmonates than the freshwater ones. It could provide a barrier to dehydration also in the head-wart cells.

A sex pheromone in the snail plays an important role in the successful achievement of copulation through their use in courtship behavior. The surface of the sex pheromone-secreting cells in insects such as *Bombyx mori* (see WAKU & SUMIMOTO, 1969) and *Choristoneura fumiferana* (see PERCY, 1974) has a microvilli surface structure. The surface of the head-wart cells also have the microvilli. The sex pheromone seems to be released by evaporation via the microvilli when the head-wart was protruded to the partner, like insects. In pulmonates, the epidermal cells have a microvilli structure (WONDRAK, 1967; 1968; ZYLSTRA, 1972). Therefore, the head-wart cells may be modified from the ordinary epithelial cells in the evolutionary processes.

It is well known that the sex pheromone in insects shows a strong attractant effect. On the other hand, the snail's pheromone is more aphrodisiac than attractant. These differences also appear in the fine structure of the gland cells. The insect's pheromone is lipoidal. Therefore, a smooth tubular endoplasmic reticulum or deformed mitochondria containing granules predominate in the pheromone-secreting cells from the time of emergence. On the other hand, the snail's pheromone is proteinaceous and is mainly synthesized by the Golgi apparatus.

The detailed fine structure of the head-wart will be published elsewhere.

ACKNOWLEDGEMENTS

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Explanation of Figures 2 to 6

(on the following three Plates)

The fine surface structures of the head-wart in the snail,
Euhadra peliomphala

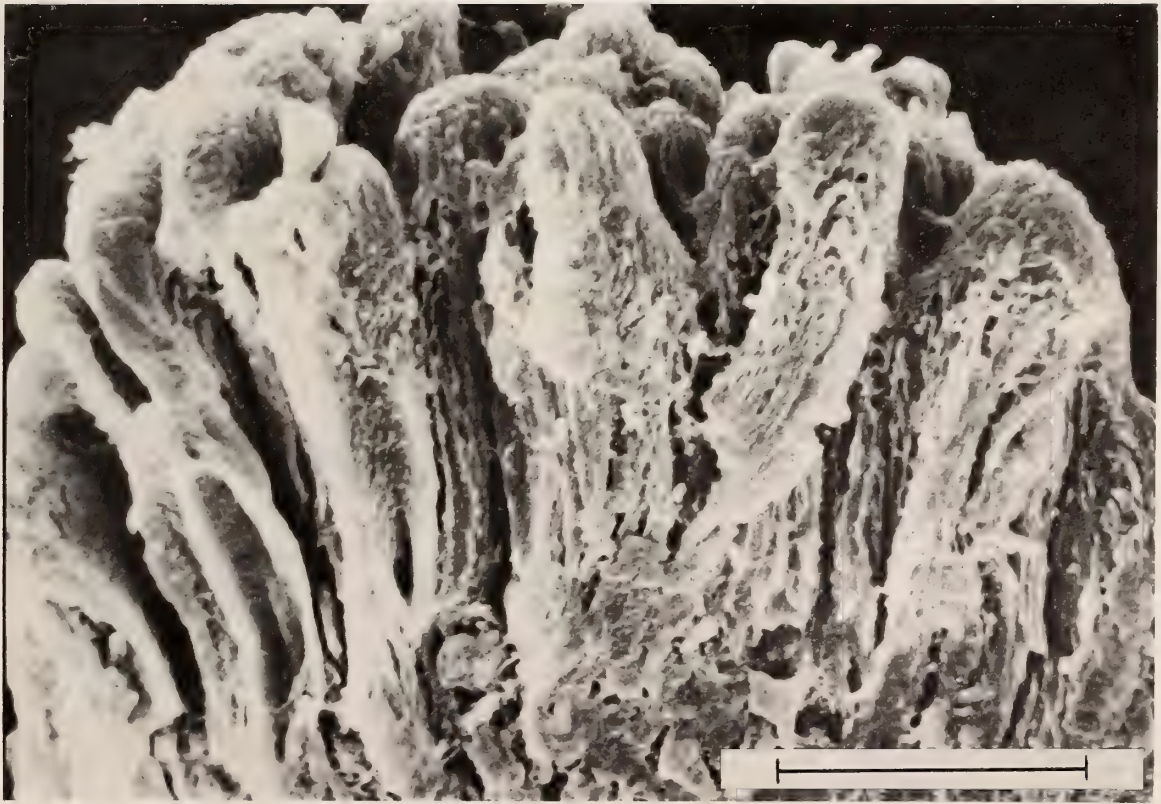
- Figure 2: Dorsal view of the head-wart Scale 25 µm
Figure 3: Lateral view of the sectioned head-wart Scale 25 µm
Figure 4: The fine structure of the head-wart cells in the snail, *Euhadra peliomphala* in the adult stage Scale 5 µm

- Figure 5: The apical region of the head-wart cell and the goblet cell Scale 1 µm
Figure 6: The head-wart cells in the snail, *Euhadra peliomphala* in the breeding season Scale 1 µm

2



3



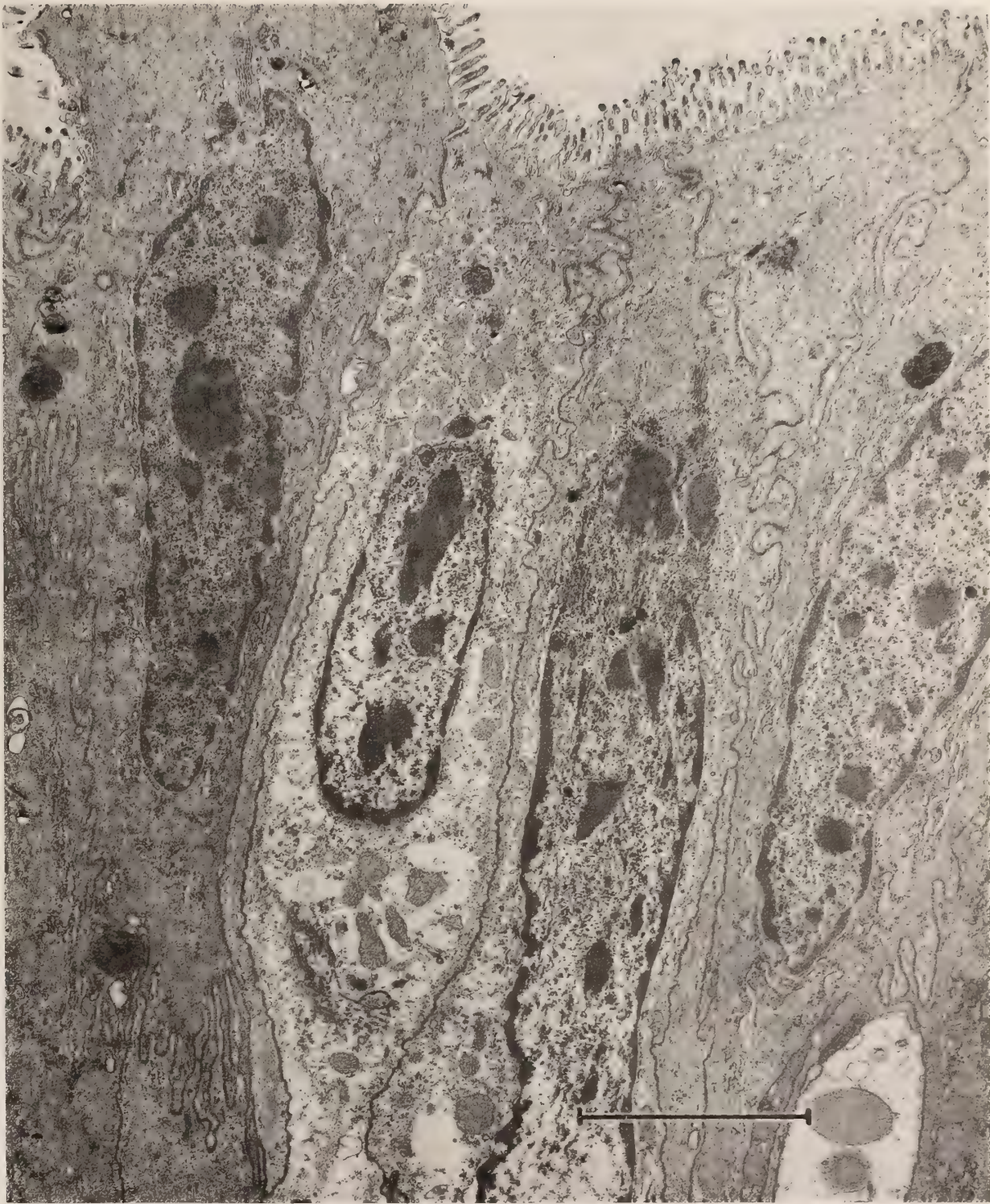


Figure 4

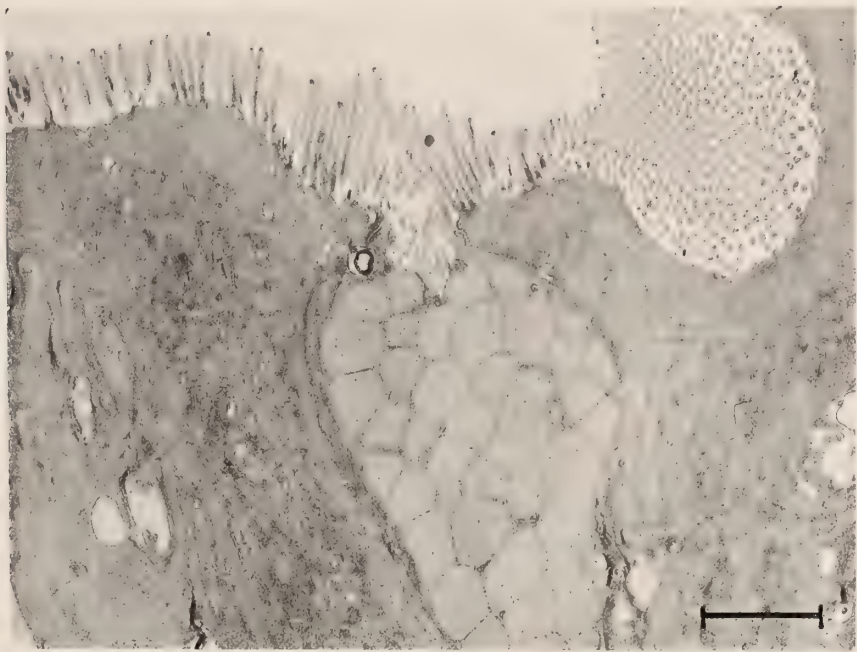


Figure 5

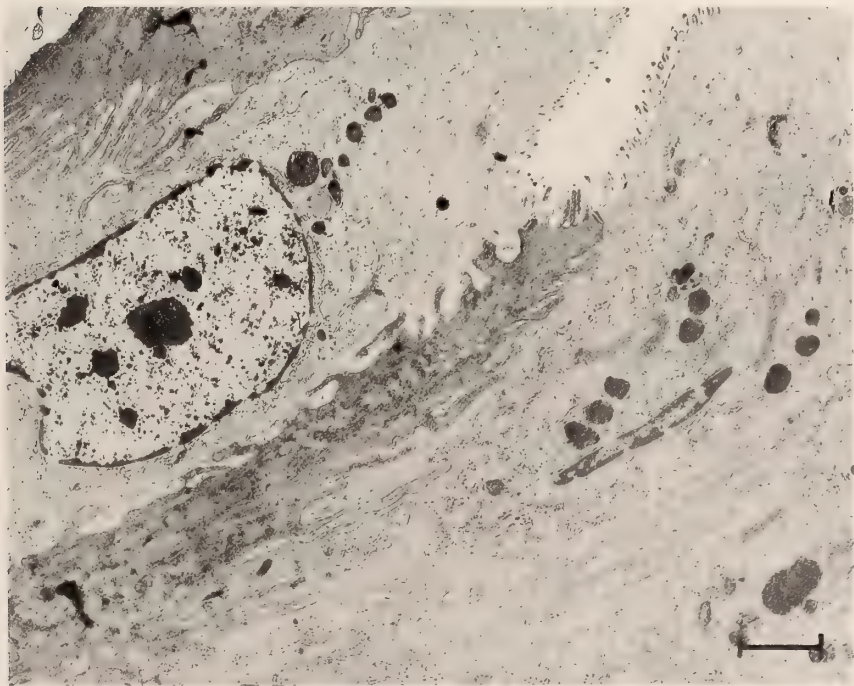


Figure 6

A Morphological and Genetic Analysis of Geographic Variation Among Oysters in the Gulf of Mexico

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INTRODUCTION

IT HAS OFTEN BEEN NOTED that oyster shells are highly variable in shape. This variation appears to correlate closely with changes in environmental variables. For instance, oysters growing singly on firm bottoms tend to develop round shells, whereas specimens living on soft bottoms usually have slender shells. Thus, variation in shell shape appears to provide information on the specific environment in which an oyster developed but is of questionable use in determining its geographic origin.

A variety of techniques have been applied to answer the question of whether geographic races of *Crassostrea virginica* (Gmelin, 1791) exist. Beginning with studies of differences in heat inducement of spawning (STAUBER, 1950; LOOSANOFF & NOMEJKO, 1951), races of *C. virginica* have been based on chromatography of peptides (HILLMAN, 1964), serological tests (LI *et al.*, 1967), and electrophoresis of enzymes (BUROKER *et al.*, 1979). These physiological and biochemical procedures provide data less influenced by environmental factors. However, there has been no study of the degree to which morphological variation reflects physiological or genetic differences. This study was undertaken to determine whether geographic races of oysters existed in the Gulf of Mexico on either side of the Mississippi River or along the Texas coast and to examine the correlation of morphological and biochemical variables in detecting geographic variation.

METHODS AND MATERIALS

Collection Methods

Five collections of oysters were made at the following localities: 1) Biloxi Bay, Mississippi, 2) West Bay, Texas, near the Galveston airport, 3) Drum Bay, Texas, 4) Aransas Bay, Texas, and 5) lower Laguna Madre (near Port Isabel), Texas. All the collections were similar in that all five came from small shallow reefs in protected bays. The oysters were sampled without regard to size or location.

Electrophoretic Analyses

The collections were taken alive to the laboratory and frozen at -60°C . In processing, the oysters were partially thawed in water, removed from the shell and allowed to drain for 15 minutes before being weighed. The right valve was saved for later analysis. The adductor muscle and part of the digestive diverticula were then placed in separate test tubes with grinding buffer (0.1M Tris, 0.001M EDTA, 0.05M CaCl_2 , 0.0005M NADP). The volume of the buffer was approximately one half that of the tissue. The tissue was then homogenized using a teflon tipped grinding bit and centrifuged for 20 minutes at 19000 rpm (46300g). The supernatant was then frozen until electrophoretic analysis could be carried out.

Starch gel electrophoresis was used to assess genetic variation (SELANDER *et al.*, 1971). Two buffer systems were used: 1) discontinuous Tris citrate (Poulik) gel; 2) lithium hydroxide gel.

Five enzyme stains were used (SELANDER *et al.*, 1971): Phosphoglucose Isomerase (PGI, EC 5.3.1.9), Phosphoglucose mutase (PGM, EC 2.7.5.1) esterase with 4-methylumbel-

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liferyl acetate as substrate (4MU EC 3.1.1), peptidase with 1-leucyl-L-alanine as substrate (Leu-Ala, EC 3.4.1), Glutamate oxaloacetate transaminase (GOT, EC 2.6.1.1). PGI, PGM, and GOT were analyzed on Poulik gels. 4MU was analyzed on LiOH gels. Leu-Ala resolved equally well on both gel types.

Each stain produced one scorable locus. At each locus the most common allozyme was designated M, those migrating faster (more anodally) F, and those slower (more cathodally) S. If more than one F or S existed, subscripts were consecutively assigned starting with the allozyme closest to M in mobility.

Morphological Analysis

Standard height and length measurements were made from the right valve for morphological comparisons (GALTISOFF, 1964). The height was measured from the tip of the beak to the outer lip along a line touching the anterior edge of the muscle scar. The length was measured on a line perpendicular to the height line through the dorsal edge of the muscle scar. The ratio of length to height was computed as a measure of shell shape (GALTISOFF, 1964). Also, all of the tissue was removed from the shell, blotted, and weighed to obtain a wet weight value.

Table 1
Allozyme frequencies.

Locus	Alleles	Biloxi Bay	West Bay	Drum Bay	Aransas Bay	Laguna Madre
PGI	F3	0.000	0.000	0.006	0.000	0.000
	F2	0.097	0.043	0.074	0.083	0.043
	F1	0.486	0.468	0.358	0.417	0.100
	M	0.389	0.473	0.534	0.431	0.557
	S1	0.028	0.016	0.006	0.056	0.186
	S1	0.000	0.000	0.023	0.014	0.017
	S3	0.000	0.000	0.000	0.000	0.043
		36 ¹	94	88	36	35
PGM	F2	0.045	0.051	0.026	0.045	0.000
	F1	0.111	0.063	0.103	0.106	0.052
	M	0.722	0.659	0.718	0.667	0.741
	S1	0.125	0.204	0.154	0.167	0.155
	S2	0.000	0.023	0.000	0.015	0.052
		36	88	78	33	29
4MU	F1	0.000	0.000	0.006	0.000	0.000
	M	0.861	0.833	0.876	0.847	0.014
	S1	0.139	0.167	0.107	0.153	0.986
	S2	0.000	0.000	0.011	0.000	0.000
		36	93	89	36	36
Leu-Ala	F3	0.014	0.011	0.028	0.000	0.014
	F2	0.186	0.269	0.244	0.186	0.222
	F1	0.243	0.199	0.189	0.333	0.250
	M	0.343	0.393	0.422	0.375	0.375
	S1	0.214	0.124	0.100	0.097	0.111
	S2	0.000	0.005	0.017	0.014	0.028
		35	93	90	36	36
GOT	F3	0.000	0.000	0.000	0.000	0.056
	F2	0.016	0.005	0.006	0.000	0.000
	F1	0.500	0.484	0.478	0.403	0.847
	M	0.469	0.493	0.517	0.583	0.097
	S1	0.016	0.016	0.000	0.014	0.000
		32	92	90	36	36

¹Number of individuals analyzed.

RESULTS

Allozyme frequencies for each locus are presented by collection in Table 1. The Laguna Madre collection is greatly different from all other collections. At the PGI locus, the F1 allozyme has a lower frequency in the Laguna Madre collection than in the others, with a concomitant increase in the S1 allozyme. The Laguna Madre collection is nearly monomorphic at the 4MU locus, and the common allozyme changes from the M to the S1 allozyme at Laguna Madre. In addition, the most frequent allele at the GOT locus is the F1 allozyme in the Laguna Madre sample, whereas the other samples have similar frequencies of the F1 and M allozymes.

Table 2

Genetic variation of oyster populations.

Population	Mean heterozygosity	Variance of heterozygosity
Biloxi Bay	0.513	0.035
West Bay	0.518	0.025
Drum Bay	0.494	0.033
Aransas Bay	0.521	0.029
Laguna Madre	0.418	0.081
Average (H_s)	0.493	

Goodness-of-fit of observed genotype frequencies to those expected from Hardy-Weinberg equilibrium was tested by a randomization computer program. The deviations that were found will be discussed in a subsequent paper (Groue and Lester, in preparation).

The amount of variation within each population was measured as heterozygosity. The heterozygosity for a locus (h) is defined as $1 - \sum x_i^2$ where x_i is the frequency of the i th allozyme, and average heterozygosity (H_s) is the mean of h over all loci examined. H_s is a good measure of diversity because it is sensitive to changes in both the number and frequencies of 'alleles' (NEI, 1975). Values for H_s as well as variances of h are presented in Table 2. The heterozygosity of the Laguna Madre sample is slightly below those of the other four, which are all similar.

Table 3

Genetic identities based on gene frequencies.

	Biloxi Bay	West Bay	Drum Bay	Aransas Bay
West Bay	0.992			
Drum Bay	0.987	0.993		
Aransas Bay	0.989	0.990	0.989	
Laguna Madre	0.641	0.659	0.640	0.628

The similarity between two populations is measured with the normalized genetic identity (I) (NEI, 1975). At the j locus this is defined as

$$I_j = \frac{\sum x_i y_i}{\sqrt{\sum x_i^2 \sum y_i^2}}$$

where x and y represent the frequencies of the i th allozyme in populations x and y , respectively. For all loci in a sample, the overall genetic identity of x and y is defined as

$$I = \frac{J_{xy}}{\sqrt{J_x J_y}}$$

where J_x , J_y and J_{xy} are the arithmetic means over all loci of $\sum x_i^2$, $\sum y_i^2$, and $\sum x_i y_i$, respectively.

The genetic identity (I) of each pair of populations is presented in Table 3. The West Bay, Drum Bay, Aransas Bay and Biloxi Bay collections are all similar with at least 98.7% of the mobility classes (alleles) being shared with other populations. Laguna Madre oysters share between 62% and 66% of the mobility classes (alleles) with other samples.

Table 4

Morphological measurements.

	Biloxi Bay	West Bay	Drum Bay	Aransas Bay	Laguna Madre
Height (cm)					
mean	7.36	6.40	6.85	8.46	5.99
S. D.	1.17	1.50	1.11	1.56	1.24
Length (cm)					
mean	5.27	4.99	4.37	4.54	3.16
S. D.	0.73	0.99	0.70	0.92	0.55
Weight (g)					
mean	13.60	11.92	9.94	12.68	6.10
S. D.	6.07	6.96	4.22	5.37	2.80
Length/height index					
mean	0.72	0.79	0.64	0.53	0.54
S. D.	0.10	0.14	0.11	0.09	0.14

Morphological Variation

The means and variances of the morphological measurements are presented in Table 4. In order to analyze differences in shape, the length/height ratio was calculated for each individual. Means and variances of this index are also presented in Table 4. The distributions of this index for each population were fitted to a normal distribution and none were found to deviate significantly ($p < 0.25$).

A one-way analysis of variance was performed on this index and significant differences between populations were found ($F = 49.34$, degrees of freedom = 4 and 287, $p < 0.001$). A Student-Newman-Keuls (SNK) test (SOKAL & ROHLF, 1969) found that only the Laguna Madre and Aransas Bay populations were not significantly different; all other combinations were significantly different.

DISCUSSION

Macrogeographic Differentiation

Previous studies have examined various forms of geographic variation in oysters and other marine bivalves and implied a genetic basis for that variation. Geographic variation was first demonstrated by STAUBER (1950) and by LOOSANOFF & NOMEJKO (1951) who found differences in the spawning reactions of populations of oysters in response to water temperature. Spawning could be induced in northern oysters by a short exposure to warm water, whereas southern oysters required a longer exposure to higher temperatures. Populations with different responses were called "physiological races."

HILLMAN (1964) used paper chromatography to demonstrate differences in the patterns of free amino acids and small peptides between two populations of *Crassostrea virginica* from Long Island Sound and the James River, Virginia. Populational differences were also found by LI *et al.* (1967). Through the use of serological techniques, they found antigenic differences between two populations from the east coast of Canada.

NEWKIRK *et al.* (1977) found that larvae of parents from a low salinity population were more tolerant to low salinity than larvae of parents from a medium salinity area. Using crosses and progeny testing, they concluded that a cytoplasmic as well as a genetic factor was affecting the salinity tolerance of larvae from these populations.

Recently, in an electrophoretic study of the genera *Crassostrea* and *Saccostrea*, BUROKER *et al.* (1979) included two collections of *C. virginica* from Nova Scotia and west Florida. These populations had low genetic similarities but intraspecific populations of other oyster species are nearly identical genetically. They suggest that the differences between these populations justify their designation as separate subspecies. The study also demonstrated that the west Florida collection and a collection of *C. rhizophorae* from the Virgin Islands were very similar, indicating that these forms are closely related.

Macrogeographic variation has been demonstrated electrophoretically in *Mytilus edulis* by KOEHN *et al.* (1976). They analyzed 6 loci in 150 samples taken along the Atlantic Coast. At the LAP locus the most common allele ($p = 0.55$ -

0.59) was uniform from Virginia to Cape Cod, where there was a sharp decrease in frequency to 0.10 which continued north. A similar decrease occurred inside Long Island Sound. The GPI (PGI) locus exhibited correlation between allele frequencies and the latitude from which samples were taken. The other loci were homogeneous across the ranges.

In the present study, little genetic variation was indicated among the four northern populations. The Laguna Madre oysters, however, are genetically different. The data are consistent with results obtained by Dr. Wyatt Anderson (personal communication). He has analyzed oyster populations from along the Gulf of Mexico and Atlantic coasts. His results show that the Laguna Madre collections differ from other Gulf collections.

The large genetic differences between the Laguna Madre collection and the others may have risen from differential selection based on environmental differences or from isolation and genetic drift of alleles. The Laguna Madre population is both the most ecologically different and the most isolated population studied. Ecologically, the oysters in the Laguna Madre area are unusual in having adapted to hypersaline conditions (BAUER, 1962). Salinities in this area are higher than 35 ppt for several months each summer. Reefs of *Crassostrea virginica* rarely survive in salinities over 25 ppt.

The oysters of the lower Laguna Madre (near Port Isabel, Texas) are separated by a distance of 400km from the nearest *Crassostrea virginica* populations in Redfish Bay, near Corpus Christi. No oysters are found in the Laguna Madre north of the Port Isabel area because of hypersalinity. Larval movement occurs by longshore currents along the Gulf side of Padre Island. Experiments by SMITH (1975) and WATSON & BEHRENS (1970) indicate that these wind-driven currents generally flow north in the summer but that net movement is low. During the winter there is often a convergence of two currents, one flowing south and one flowing north at the central portion of Padre Island. These studies suggest a low potential for migration between the lower Laguna Madre and oyster reefs to the north.

Comparison of Genetic and Morphological Differences

The pattern of genetic variation among collections is quite different from that of morphological variation. Morphologically, each population is distinguishable as indicated by shell measurements and other shell characteristics which cannot be easily quantified. The morphological variation is probably more closely related to environmental differences. It has long been known that the environment can

affect growth and shell characteristics of oysters. An experienced commercial oysterman can often determine the local origin of a catch of oysters merely by noting their shape, size, color and size of clusters. Factors which are known to affect these characteristics are salinity, current flow, turbidity and substrate (GALTISOFF, 1964). Transplanted oysters can take on the characteristics of their new environment, which indicates a small genetic component to the morphological variation.

Of the five collections of oysters, the Laguna Madre collection looks the most different. These oysters had long, narrow, thin, crenulated, and highly colored shells. They formed larger clusters than usual. Cluster size and coloration could be used to distinguish the Laguna Madre and Aransas Bay collections even though the shapes of the oysters were not significantly different. The odd appearance of oysters from the Laguna Madre area was noted in several earlier papers (HEDGPETH, 1953 and BAUER, 1962). PARKER (1955) reported evidence that the appearance is due to the environmental effect of hypersalinity. In a study of oyster growth in Aransas Bay, he found that oysters rapidly added new pigmented shell in response to high salinities which resulted from a two year drought. Periodic high salinity in Aransas Bay may explain the similarity in growth patterns of the Aransas Bay and Laguna Madre collections as indicated by the length/height index (Table 4).

Generally, this study shows that morphological and genetic variation are not related. The four northern populations were significantly different morphologically, but not genetically. The morphological variation is probably a response to differences in environmental factors such as salinity. The genetic variation does not seem to be related to these environmental differences.

SUMMARY

Oysters collected at five sites from Biloxi Bay, Mississippi to the Laguna Madre at the southern tip of Texas were analyzed for shell shape and five biochemical genetic markers. A statistical test showed that all of the samples were significantly different in morphology except the two

most southern collections from the Laguna Madre and Aransas Bay, Texas. However, the statistical analysis of the biochemical genetic data demonstrates the genetic identity of all of the collections, except the one from the Laguna Madre. It is concluded that shell morphology is useful for determining environmental differences among oyster populations, but biochemical or genetic characters, or both, are necessary to study geographic differentiation in oysters.

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Notes on Living *Casmaria vibexmexicana* (Stearns, 1894)

BY

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THE ISLANDS OF PANAMA BAY, Panama, with their calcareous substrate, form the ecological habitat for *Casmaria vibexmexicana* (Stearns, 1894). Specimens were observed from 1976 through 1981 living intertidally. This is the first report of the species being taken alive in numbers. Collections were made on midnight tides of -60 and -90 cm on a sloping sand beach where the mollusks were either "bumping" or gliding about on the surface in several inches of water. A companion paper will present material on radular studies of a small number of the specimens.

The genus *Casmaria* Adams and Adams, 1853 is represented by several varieties worldwide. Their systematic status, however, has been debated. The species are very similar in appearance but show some differences in shell and soft part morphology.

DODGE (1956: 185-188), in his work on Linnean types, tended to make *Casmaria erinaceus* (Linnaeus, 1758) a subspecies of *C. vibex* (Linnaeus, 1758) since the latter is the designated type of *Casmaria*. R. T. ABBOTT (1968: 189-201) accepts two species, *Casmaria erinaceus* (Linnaeus, 1758), with two subspecies, *C. e. kalosmodix* (Melvill, 1883) and *C. e. vibexmexicana* (Stearns, 1894), and *Casmaria ponderosa* (Gmelin, 1791), with four subspecies, *C. p. perryi* (Iredale, 1912), *C. p. unicolor* (Dautzenberg, 1926), *C. p. atlantica* (Clench, 1944), and *C. p. nipponensis* Abbott, 1968. The various so-called subspecies accepted by Abbott seem to be based on geographical localities rather than on morphological differences. TINKER (1958: 86), in his book on shells of Hawaii and the south seas, recognizes three forms, *Casmaria erinaceus*, *C. erinaceus kalosmodix*, and *C. ponderosa*. VERMEIJ (1978: 272) lists *Casmaria atlantica* from the western Atlantic and *C. vibexmexicana* from the eastern Pacific as cognates. According to Keen (pers. comm.), "When Stearns named a cassid rather ambiguously as *vibex-mexicana* he did not clearly state that this was a subspecies of its Indo-Pacific counterpart; so, under our modern code the name would be written without the hyphen and treated as a separate species."

It is not the intention to compare here the relative merits of the so-called various subspecies, but rather to present current evidence of living specimens of *Casmaria vibex-*

mexicana and subsequent radular studies (see related paper this issue).

The following records of dead-taken specimens are included to indicate possible localities where the Stearns species might be taken alive. EMERSON & OLD (April 1963: 144; plt. 10) record one specimen in the McKibbin collection, from Lobos Island, Gulf of California, Mexico taken in 6 m of water (Keen, 1971; color plate XVI, figs. 5, 6). The same authors (September 1963: 14-16; figs. 12, 13) report two beach specimens, one from the Tres Marias Islands, Mexico and one from Santa Catalina Island, Gulf of California, Mexico. In addition, one beach specimen in the Donald Shasky collection is from Maria Cleofas Island, Tres Marias Islands, Mexico as is another specimen in the Helen DuShane collection. Also, in the DuShane collection are two dead-collected specimens from the La Paz area, Gulf of California, Mexico. Three specimens taken at Rancho Buena Vista, Las Palmas Bay, Mexico are in the collection of the Santa Barbara Museum of Natural History as is one from the same locality in the Stanford collection (now at the California Academy of Sciences). ALEX KERSTITCH (1976) reported a specimen from Cabo San Lucas, Gulf of California, Mexico. The San Diego Natural History Museum has one specimen in the H. N. Lowe collection taken at San Jose Island, Gulf of California, Mexico. The author has seen one other specimen from San José Island and one taken by Lawrence Thomas diving in approximately 6 m of water at Cuastecomate Bay, Jalisco, Mexico. The records listed above would indicate that the species occurs living in somewhat shallow water and is coral reef associated, since the localities from which those specimens have been taken are in areas where living coral is present. The range indicated for this species is from the Gulf of California, south along the west Mexican coast, Costa Rica, Panama Bay, and the Galápagos Islands (ABBOTT, 1968; KEEN, 1971; KERSTITCH, 1976).

A number of supposedly live-taken specimens have been reported from time to time, but documentation of live specimens is somewhat doubtful unless the animal is in the shell. For this reason these records are not being published here.

Because of possible exploitation of the molluscan fauna, station numbers will be used in this paper for identifying the several small islands in Panama Bay, Republic of

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Panama. In 1976 two live specimens were taken by Joe Buelna on a small reef of Station 1. This is the only report of live specimens being taken in a mixture of sand and mud substrate. In March 1978 one live-taken specimen was obtained by Captain Richard Callaway on the beach at this same station. It measures 60 mm in length, 35 mm in width. In 1978 Dave Drennan and others took a number of specimens at Station 2 on a small beach. During 1979, the following collectors took additional live specimens on a coral sand beach at Station 3: Richard Callaway, Helen DuShane, John McQueen, Donald Shasky. The shells measure length, 41.8 mm to 63 mm, width, 27.3 mm to 39.6 mm. In February 1980, on a small, sloping, calcareous, sand beach with a southern exposure, Richard Callaway took a few more specimens at Station 3, with measurements of length, 52.3 mm to 58.1 mm, width, 30.0 mm to 34.9 mm.

On April 7, 1981 Archibald, native and captain of our boat, took two specimens during a -63 cm tide, on the upper portion of the beach at Station 3, buried $7\frac{1}{2}$ to 12 $\frac{1}{2}$ cm in sand, 45 to 60 minutes after low tide, at approximately 12:45 p.m. This seems to be the only record of *Casmaria vibexmexicana* having been taken during daylight hours. The two specimens measure length, 48.5 mm, width, 33.2 mm, and length, 50 mm, width, 35 mm and are now in the Barbara Corner collection.

During April 1981 more specimens were taken alive on a small island coral reef in Panama Bay at Station 4. Again, the midnight tide was extremely low (-75 cm) with specimens "bumping" on a small sand beach. The following collectors took specimens that measure 40.7 mm to 64.5 mm in length and 21.5 mm to 40.5 mm in width: Rosemary Adams, Richard Callaway, Barbara Corner, Helen DuShane, John McQueen, Donald Shasky and Gil Williams. One observation of interest is the "bump" in the sand. Anywhere from 5 to 12.5 cm below the surface under the "bump" a specimen might be taken, but further excavation usually revealed another smaller specimen just below the first. Whether this is a spawning activity or not remains to be verified.

At all locations specimens were collected from one hour and fifteen minutes before low tide to one hour after low tide. Sometimes the mollusks were buried 5 to 7 $\frac{1}{2}$ cm in dry sand about 30 cm above high tide line down to 20 to 30 cm of water with animals in the process of burying into the substrate with no trace of trails. The mollusks were collected on the south side of all four stations; with minus tides of 60 to 90 cm from 11:22 p.m. to 12:07 a.m., with the exception of the two collected during daylight hours.

Gil Williams reports that *Casmaria vibexmexicana* feeds on the small epifaunal and burrowing echinoid sea biscuit, identified tentatively as *Lovenia cordiformis* A. Agassiz, 1872 and prefers a calcareous substrate, while the closely related

mollusk, *Cassis centiquadrata* (Valenciennes, 1832) feeds on a large sand dollar and prefers a sand-mud mixture habitat. *Casmaria vibexmexicana* is collected year-round, while *Cassis centiquadrata* is found in the intertidal zone only occasionally, but in great numbers. The type of larval dispersal for the former species is unknown. At Station 3, DuShane (1965), while looking for an epitoniid, *Asperiscala billeeana* (DuShane and Bratcher, 1965), collected larvae of *Cassis centiquadrata* on the zooids of *Tubastrea tenuilamellosa* (Milne-Edwards and Haime, 1848). HUGHES & HUGHES (1981), reviewed, from published data, the anatomy of the feeding apparatus, diet, and feeding behavior of the Cassidae, observations not at variance with those presented here.

Specimens in alcohol have been placed with the following museums: American Museum of Natural History, New York City; Academy of Natural Sciences, Philadelphia; Los Angeles County Museum of Natural History, California; and the United States National Museum, Washington, D.C.

The animal of *Casmaria vibexmexicana* has not been described before. The foot is white; the head has white, outcurved tentacles, on the outer base of which are black eyes, on short, bulbous eye stalks. The inhalant siphon protrudes from a narrow extension of the aperture, the siphonal canal. This flexible, tubelike organ contains epithelial cells capable of secreting calcareous shell. Since *Casmaria* has no periostracum the mantle edge is smooth and lacks the supramarginal groove necessary for mollusks with a periostracum. As the animal propels itself along the surface of the sand, a series of small muscular wave-like motions can be observed. The golden-yellow, fan-shaped operculum, borne on the rear dorsal surface of the foot, is horny, as in other cassids. The inner side has three small reinforcement bars. The outer side is smooth.

Enough live-taken specimens have been seen to make it possible to describe variation in shell color. The color ranges from a pale pink-tan with barely perceptible banding to dark gray-mauve-brown well-banded forms, with a fine brown line outlining the bands. Small, black pinpoint specks also outline the spiral color bands on most specimens, but there are occasional ones where the specks are almost non-existent. On these the color banding is pale. The pinpoint specks also follow the axial growth stages. The color of the aperture is white on the lighter colored shells and deepens to a chestnut shade on the darker ones. The outer lip has 4 to 5 denticles, with longitudinal brown markings on the upper portion of the outer lip and one brown-black mark on the siphonal canal.

It would be premature at this point to rank the taxa within *Casmaria* as truly distinct species or subspecies. The small differences in shell morphology and radular characteristics might be the result of geographical variation. At present one can only speculate about pathways of dispersal and the morphological adaptations that have taken place.

One specimen in the DuShane collection, and two in the Williams collection, from Station 4, have the low tubercles at the shoulder whorl that are supposedly one of the identifying characters of *C. ponderosa*, the range of which is limited to the Hawaiian Chain and Polynesia. Many specimens would be required to establish intraspecific variation within the species. While these observations are preliminary, this author thinks it productive to bring these findings to the attention of other workers with the hope that the effort will aid in future systematic studies of the species.

ACKNOWLEDGMENTS

Sincere thanks go to Renée DuShane for reading the original manuscript and giving succinct advice; to Dr. Myra Keen, Professor Emeritus, Stanford University, for a critical review of the paper; to Richard Callaway, Barbara Corner and Gil Williams for observations on the habitat, ecology and feeding habits of cassids; to the many collectors whose cooperation is appreciated; and to Dr. William K. Emerson for assistance with published material difficult for me to obtain otherwise.

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Optical and SEM Comparison of *Casmaria erinaceus* (Linnaeus, 1758) and *C. vibexmexicana* (Stearns, 1894)

BY

HUGH BRADNER¹ AND HELEN DuSHANE²

(3 Plates)

THE RECENT AVAILABILITY (DuShane, 1982) of live-collected specimens of the rare *Casmaria vibexmexicana* (Stearns, 1894) has permitted comparison with the relatively common *C. erinaceus*, (Linnaeus, 1758). The restricted range of *C. vibexmexicana* might imply some different anatomical characteristics from the widely dispersed *C. erinaceus* even though the shells are very similar. This situation had been reported by BRADNER (1979), for example, in *Cypraea isabellamexicana* (Stearns, 1893) vs. the common Indopacific *Cypraea isabella* (Linnaeus, 1758).

Casmaria erinaceus, a bonnet shell, is widely distributed throughout the tropical Pacific, Red Sea, and East Africa, through Melanesia and Micronesia; while enough living and beach specimens of *C. vibexmexicana* have been found to establish its range as probably limited to the region between the southern part of Baja California and Panama and perhaps to the Galápagos Islands. Until very recently, no living specimens had been collected. The 1963 report of the Puritan-American expedition (EMERSON & OLD) and an *Indo-Pacific Mollusca* article on the genus *Casmaria* by ABBOTT (1978) both comment on the absence of live specimens. In *Sea Shells of Tropical West America*, KEEN (1971) calls it "an elegant and very rare mollusk." The color plate in this definitive book shows a shell whose markings seem distinguishably different from the usual illustrations of *C. erinaceus*. ABBOTT (1968) recognized two members of the genus *Casmaria*: The first member is *C. erinaceus*, with subspecies *C. erinaceus erinaceus* and *C. E. vibexmexicana* and "with some hesitancy" *C. E. kalosmodix* (Melville, 1883) in the Hawaiian chain and Polynesia. The second member of the genus is *C. ponderosa* (Gmelin, 1791) with subspecies *C. ponderosa atlantica* (Clench, 1944). It will not be discussed here.

ABBOTT (1968) says of the *Casmaria erinaceus*, "This widely distributed, moderately common *Casmaria* called *vibex* Linnaeus, by some workers, is quite variable in sculpturing and coloring, and in some cases is difficult to distinguish from *ponderosa* (Gmelin). It occurs in two forms, often

with intergrades, throughout most parts of its range—the typical heavy, smaller *erinaceus* with nodules on the shoulder, and the smooth, usually larger, lighter form, *vibex* Linnaeus."

The extensive synonymy of these species will not be discussed; reference will simply be made to *Casmaria erinaceus*, *C. vibexmexicana*, and *C. kalosmodix*.

Four *Casmaria vibexmexicana* radulae and six live-collected *C. vibexmexicana* shells were available for study. Animals from the "relatively common" *C. erinaceus* were hard to find; the six available live-collected specimens yielded only two radulae.³ No *C. kalosmodix* animals were obtained.

VISUAL/OPTICAL OBSERVATIONS

The shells of *Casmaria vibexmexicana* and *C. erinaceus* were indistinguishable except possibly for markings and size: Five of the *C. vibexmexicana* clearly showed rows of brown dots in a well-defined beautiful pattern, as in the KEEN color plate (1971: XVI, nos. 5, 6). The sixth did not have easily visible dots; it was very much like all of the *C. erinaceus* specimens. The difference between the two populations might tentatively be thought significant except for ABBOTT's (1968) statement that *C. erinaceus* usually has axial rows of very tiny "fly speck" dots on the coarse growth lines of the body whorl. The homogeneity of the *C. erinaceus* population of the present study apparently was anomalous.

The average size of specimens of *Casmaria vibexmexicana* is slightly larger than *C. erinaceus*, although there is an overlap between small *C. vibexmexicana* and large *C. erinaceus*. All twelve specimens of the two species are essentially identical in shape. Visual comparison of protoconchs did not show any distinguishable difference; nor did photomicrographs of five *C. erinaceus* vs. one *C. vibexmexicana* protoconch.

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³ Five *Casmaria erinaceus* shells and the two radulae were from Jolo Is., Sulu Archipelago, Philippines. The sixth shell had no collection data other than Philippines.

Visual comparisons of opercula showed no evident differences.

SEM OBSERVATIONS

The *Casmaria* radula is very short, about 5 mm in a 60 mm shell. It is taenioglossate; i.e., seven teeth per row consisting of one central tooth flanked on each side by three progressively more elongated teeth (Figure 1). The teeth are usually called central (or median), lateral, inner marginal, and outer marginal.

In *Casmaria* the central and lateral teeth have well defined comblike tips, referred to as denticles, while the inner and outer marginal teeth have tips that may better be called fingers. Figure 1 (*Casmaria vibexmexicana*) shows the central teeth flanked by the laterals, and the much longer, more delicate marginals. The radula has been splayed out to exhibit these characteristics. Note that the innermost denticle of the lateral teeth is much larger than the others. SEM photographs can sometimes be misleading unless the teeth are shown at a number of angles. This occurs automatically if the sample is mounted on a curved stub, but further perspective is sometimes obtained by displaying a long segment of the radula and by the splaying of the marginal teeth. Figures 1 and 2, both taken at 70 diameters magnification, show the very similar characteristics of two *C. vibexmexicana* specimens.

Figure 3, at 200 diameters magnification, shows that the central and lateral teeth of a third *Casmaria vibexmexicana* specimen are also substantially identical to the previous ones. There is a small difference in denticle count, which will be discussed later.

The fourth *Casmaria vibexmexicana* specimen, also photographed at 200 diameters magnification, is markedly different from the others (Figure 4). There is no well-defined

symmetry, which would characterize a central row. The denticles and fingers of all teeth except perhaps the marginals on one side are badly deformed. This is not an immature section of the radula. It is an aberrant distorted specimen.

Figure 5, the first *Casmaria vibexmexicana* specimen, at 500 diameters magnification shows the highly symmetrical character of the central teeth, while Figure 6, at 200 diameters magnification shows the long delicate shape and three-fingered tips of the marginals on the specimen. Note that the inner and outer marginals lie in two well-defined rows whose bases are interdigitated. Note also that the teeth in the two marginal rows are practically identical.

Figures 7 and 8 show details at 200 diameters magnification on the two specimens of *Casmaria erinaceus*. They are very similar to each other, and again very similar to the first three *C. vibexmexicana*.

Views at 700 diameters magnification allow close examination of the lateral tooth denticles on the two *Casmaria erinaceus* specimens (Figures 9 and 10).

Careful count of the denticles and fingers of all specimens show that there are small differences as indicated in Table 1. The denticle count on the central teeth of the

Table 1

Tooth comparisons of *Casmaria erinaceus* (ER)
vs. *Casmaria vibexmexicana* (VM)

	Number of denticles or fingers					
	ER1	ER2	VM1	VM2	VM3	VM4
Central	11	11	11-13	11	11	¹
Lateral	8-9	8-9	8-10 ²	8-9	8-9	¹
Inner marginal	3	3	3	3	3	3
Outer marginal	3	3	3	3	3	3

¹Has extra row of teeth.

²Right side consistently has one more denticle than left side.

Explanation of Figures 1 to 3

Figure 1: *Casmaria vibexmexicana* No. 1; 70×
Figure 2: *Casmaria vibexmexicana* No. 2; 70×
Figure 3: *Casmaria vibexmexicana* No. 3; 200×

Explanation of Figures 4 to 6

Figure 4: *Casmaria vibexmexicana* No. 4; 200×
Figure 5: *Casmaria vibexmexicana* No. 1; 500×
Figure 6: *Casmaria vibexmexicana* No. 1; 200×

Explanation of Figures 7 to 10

Figure 7: *Casmaria erinaceus*, specimen No. 1; 200×
Figure 8: *Casmaria erinaceus*, specimen No. 2; 200×
Figure 9: *Casmaria erinaceus*, specimen No. 1; 700×
Figure 10: *Casmaria erinaceus*, specimen No. 2; 700×

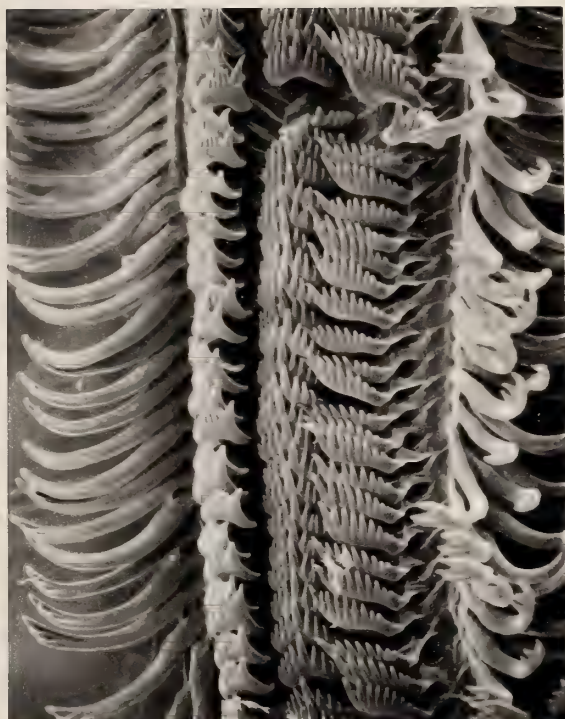


Figure 1



Figure 2

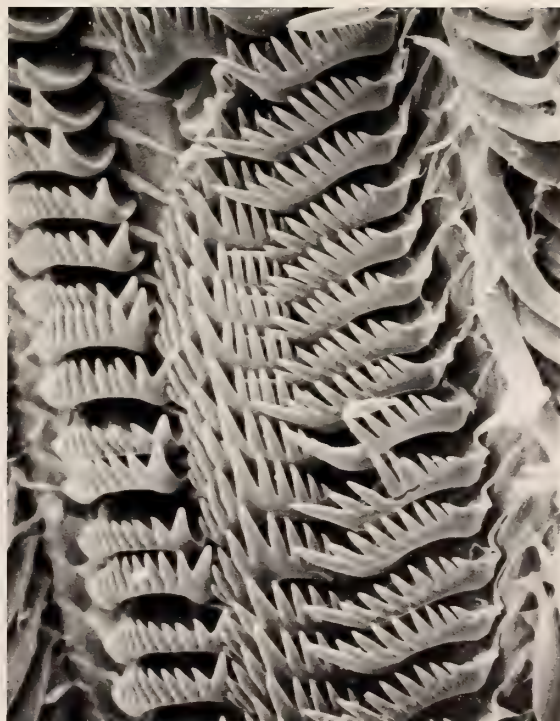


Figure 3



Figure 4

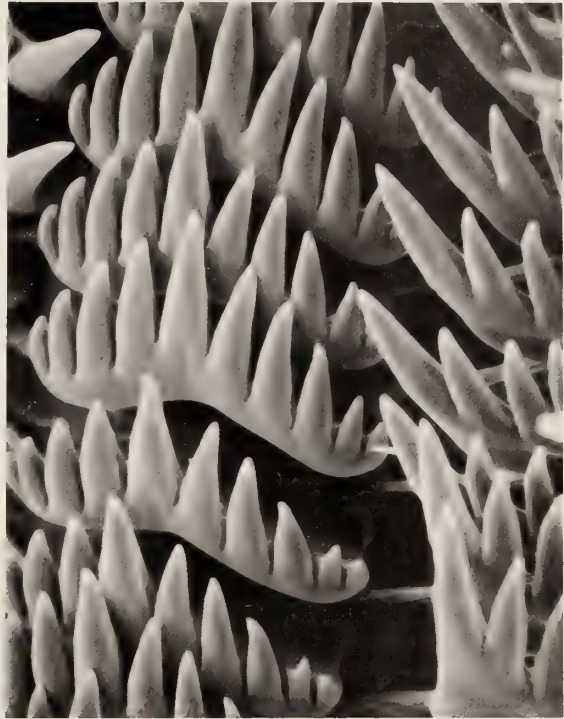


Figure 5



Figure 6



Figure 7



Figure 8



Figure 9



Figure 10

first *Casmaria vibexmexicana* specimen was not consistently 11; some teeth had 13 denticles. The lateral count was very consistent among the specimens except for VM-1 in which the right lateral consistently had one more denticle than did the left lateral. The comparisons do not include VM4, which has the extra row of teeth and multiple, variable, badly deformed shape.

Thus the SEM radula studies show greater intra-species variation than inter-species differentiation.

CONCLUSION

In summary it can be said that these specimens do not support the hypothesis that *Casmaria erinaceus* and *C. vibexmexicana* are distinct species. Much larger numbers of shells and animals are required before an unequivocal statement can be made.

ACKNOWLEDGMENTS

This study was initiated by the junior author who procured live-taken specimens of *Casmaria erinaceus* through the kindness of Dr. Robert Robertson. Live-taken specimens of *C. vibexmexicana* were provided by Richard Callaway and the junior author. *C. vibexmexicana* specimens without visible dots are in the collections of Donald Shasky and Helen DuShane. David Mulliner helped with first radula extraction and made photomicrographs of protoconchs. They, as well as Anthony d'Attilio, gave valuable counsel on many aspects of the study. The scanning electron microscope was made available by Science Applications, Inc. of La Jolla, California.

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European Land Mollusks in the San Francisco Bay Area, California:

Carychium minimum Müller and the *Arion hortensis* Complex

BY

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1. *Carychium minimum* Müller

ON FEBRUARY 12, 1981, my son and I celebrated Darwin's birthday by hunting land mollusks in San Francisco's Golden Gate Park. In humus in the tree fern dell, on the south side of John F. Kennedy Drive southwest of the Conservatory, we discovered numerous specimens of the minute snail *Carychium minimum* Müller, 1774. The circumstances of this occurrence clearly indicate that *C. minimum* was synanthropically introduced. The species is widespread from western Europe to northern Iran (WATSON & VERDCOURT, 1953) and—one published record to the contrary—is not otherwise known in North America.

The tree fern dell consists mainly of specimen trees of *Dicksonia squarrosa* averaging 3-5m tall and planted about 2-3m apart. The ground is carpeted by a loose cover of creeping buttercup (*Ranunculus repens*), Indian strawberry (*Fragaria indica*), and herb robert (*Geranium robertianum*), with scattered clumps of common calla (*Zantedeschia aethiopica*) and bears' breech (*Acanthus mollis*). Periodically the dell receives applications of compost and wood chips mainly derived from maintenance operations elsewhere in the park. It is irrigated by a sprinkler system installed high enough that the uppermost fern fronds receive the benefit of the spray. Humus 6-10cm deep lies on a fine sandy loam of pH 6.7 (mean of 13 measurements; s.d. 0.33; determined with a LaMotte ST-1001-M soil test kit). Living *Carychium* were found throughout the humus below the dry topmost layer and on the soil surface.

An additional lot of seven shells collected by J. T. Carlton in January 1970 at the margin of Lake Merritt, Oakland, following a period of heavy rains (California Academy of Sciences Department of Invertebrate Zoology, CAS 024705) closely resembles the San Francisco specimens and suggests that *C. minimum* may be more widely naturalized in suitable habitats in the San Francisco Bay area.

Dr. N. J. Evans and Mr. F. Naggs, British Museum (Natural History), have confirmed the identification of specimens from the San Francisco site. Voucher specimens are on deposit in the California Academy of Sciences (CAS 024710) and the BM(NH).

The San Francisco Bay area occurrences are well south of the native range of the genus on the Pacific coast. According to PILSBRY (1948), *Carychium occidentale* Pilsbry, 1891, ranges from Vancouver Island, British Columbia, to Ragged Canyon, 5mi (8km) south of Crescent City, Del Norte County, California. A lot collected by J. Helfer in May 1955 (CAS 024706) extends the range of *C. occidentale* south to Little River, Mendocino County, California, approximately 200km north of San Francisco.

Carychium minimum is well figured by KERNEY & CAMERON (1979): 57; figs. A, B). It differs from the native west American *C. occidentale* in being smaller (length 1.6-1.9mm compared to 2.1-2.7mm) and having fewer than five whorls when mature. The columellar fold of *C. occidentale* is less well developed, often scarcely visible in apertural view. KERNEY & CAMERON (1979:58) distinguish the similar, European *Carychium tridentatum* (Risso, 1826) from *C. minimum* as follows: "Shell relatively taller, narrower and more conical than *C. minimum*, with rather more tumid whorls; mouth-edge more thickened and teeth more prominent. The parietal fold has a different form: the expanded part is distinctly flared and in profile shows a characteristic *double flexure*. Shell colourless, growth-lines stronger and more regular than in *C. minimum*, making fresh shells appear somewhat less glossy and translucent." The internal shape of the parietal lamella is the feature most clearly separating these two species and is often best seen by breaking away the face of the body whorl with the point of a needle.

The only other published record of *Carychium minimum* as an introduction in the New World is that from a greenhouse at Norfolk Downs, Quincy, Massachusetts (CLAPP, 1912; WINSLOW, 1922; PILSBRY, 1948; DUNDEE, 1974). All of these references pertain to the same occurrence. Winslow received her specimens from G. H. Clapp, and Pilsbry and Dundee merely repeated the record. However, the shell from Norfolk Downs illustrated by WINSLOW (1922: plt. 4, figs. 18, 19) is *Carychium tridentatum*, having the upwardly deflected parietal lamella of that species (compare WATSON & VERDCOURT, 1953: plt. 10, fig. 4; and KERNEY & CAMERON, 1979: 58, fig. B). Until the study by WATSON

& VERDCOURT (1953), many authors viewed *C. tridentatum* as a variety of *C. minimum*, possibly an ecological form expressed in drier habitats. Watson and Verdcourt, however, found that the two forms maintain their morphologic distinctness even in habitats of intermediate dryness, both in Britain and on the Continent. As they noted, misidentifications of the two have been common, and even THIELE (1931) figured *C. tridentatum* as *C. minimum* in his "Handbuch der systematischen Weichtierkunde." The status of the two as separate species is now generally accepted (GODAN, 1979; KERNEY & CAMERON, 1979).

In its native range, *Carychium minimum* lives mainly in marshes and other wet places. EVANS (1972: 131) described it as "essentially a marsh species [which] very occasionally occurs in drier habitats" and (295) an "obligatory hygrophile." In contrast, *C. tridentatum* is usually found among dead leaves in woods of beech and other deciduous trees and also among coarse grass and other herbage. Both species live together "in varying proportions near the edges of rivers, ponds, or marshes, and in other places of a more or less intermediate character" (WATSON & VERDCOURT, 1953: 318).

Its dependence on perennial moisture may tend to limit the spread of *Carychium minimum* in central California to irrigated areas such as parks and gardens. Moist stream-banks may also prove to be suitable habitat. Like other minute land mollusks, it is undoubtedly transported readily from place to place undetected in soil or compost. Although *C. minimum* is found in gardens and greenhouses in Europe (GODAN, 1979) there is little indication that it is a horticultural pest of any economic importance.

2. The *Arion hortensis* Complex

Records of the European slug *Arion (Kobeltia) hortensis* Férussac, 1819, as an introduction in the New World go back at least as far as BINNEY (1842). DUNDEE (1974) listed numerous findings of the species in the eastern United States and Canada. The diagnosis of many slug taxa, however, was poorly understood until relatively recently, and many of the earlier records have been challenged or discredited.

On the Pacific Coast, *Arion hortensis* was first reported from Seattle by RANDOLPH (1896), by WASTE (1940, MS; nurseries in Oakland and Niles, Alameda County, California), then by LANGE (1944; "in greenhouses... San Francisco bay region"), possibly from inspection of Waste's manuscript report. PILSBRY (1948) repeated these records, stating that all Californian specimens seen by him were small and sexually immature—hence presumably not determinable with certainty. Although the species was not known to him at the time of his first report on introduced

mollusks of California (HANNA, 1939), HANNA (1966) was later able to summarize additional records from pest detection literature: Crescent City, Sacramento, Santa Cruz, San Anselmo, Mill Valley, and San Rafael. INGRAM & LOTZ (1950) added Golden Gate Park in San Francisco to the list of localities. ROLLO & WELLINGTON (1975) found *A. hortensis* numerous in Vancouver, British Columbia, and vicinity. I have located no records for southern California or the arid southwestern states.

DAVIES (1977, 1979) has shown that in the British Isles the "*Arion hortensis*" of popular usage actually consists of three similar but distinct species: true *A. hortensis*, *Arion distinctus* Mabille, 1868, and *Arion owenii* Davies, 1979. The three differ from one another in details of external appearance, genital anatomy, spermatophore morphology, and habits. Their geographic ranges apparently overlap extensively. All previous records of "*Arion hortensis*" need to be reexamined in the light of these findings.

In order to determine the identity of the San Francisco Bay area occurrences, I dissected material from the collections of the Department of Invertebrate Zoology, California Academy of Sciences, including voucher specimens from WASTE's (1940) report and other more recently collected material. Waste did not specify his preservation technique; the specimens are now stored in 75% ethanol. Newly collected specimens were drowned in water; then transferred in stages to 75% ethanol. Identification was based mainly on relative proportions of free oviduct and epiphallus, thick-walled (medial) and cavernous (lower) parts of oviduct, and form of the small structures at the insertion of epiphallus upon the atrium, as illustrated by DAVIES (1977: figs. 4, 5). External characters were considered secondarily. In one case the presence of a distinctive spermatophore aided the diagnosis.

The results of the dissections, summarized below, show the presence of two species, *Arion hortensis* in Marin, San Francisco, and Alameda counties, and *A. distinctus* in Contra Costa and Alameda counties. All samples consisted solely of one species; no mixed samples were found. The specimens that furnished the basis for WASTE's (1940) reports of *A. hortensis* from Oakland and Niles (repeated by PILSBRY, 1948, and HANNA, 1966) prove to be *A. distinctus*.

Arion hortensis FÉRUSSAC. MARIN COUNTY: Audubon Canyon Ranch, Bolinas Lagoon, D. Cavagnaro coll. 25 March 1975, 9 specimens (CAS 000859). SAN FRANCISCO CITY AND COUNTY: Golden Gate Park, G. D. Hanna and A. G. Smith coll. 7 November 1941, one specimen (CAS 025615). Near North American Hall of California Academy of Sciences, Golden Gate Park, A. G. Smith coll. 5 September 1942, 14 specimens (CAS 025612). Same locality, A. G. Smith coll. 9 January 1948, 5 specimens (CAS 025611); one with short, posteriorly hooked spermatophore with serrate longitudinal ridge and plate-like collar (cf. DAVIES, 1977: fig. 2d-f). Tree fern dell, south side of John F. Kennedy Drive, Golden Gate Park, B. Roth coll. 21 November 1980, 16 specimens (CAS 025566); identification con-

firmed by Stella M. Davies. "Guam Village," Alemany Boulevard near Bayshore Highway, in trash piles, A. G. Smith and G. D. Hanna coll. 30 November 1947, 2 specimens (CAS 025617). ALAMEDA COUNTY: Garden at 1735 Vine Street, Berkeley, B. Roth and G. Hefta coll. May 1980, 4 specimens (CAS 021239).

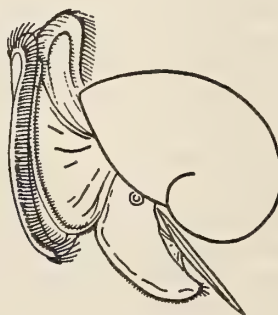
Arion distinctus Mabilie. CONTRA COSTA COUNTY: Garden at 267 Amherst Avenue, Kensington, M. Schmelzer coll. January-February 1981, 9 specimens (CAS 021240). Same locality and collector, March 1981, one specimen (CAS 021238). Same locality and collector, May 1981, 3 specimens (CAS 025613). ALAMEDA COUNTY: California Nursery Company, Niles, R. J. Waste coll. 22 July 1939, one specimen (CAS 025620). Nursery in Niles, coll. 10 February 1940, 2 specimens (CAS 025616). Nursery in Oakland, coll. 5 March 1940, 1 specimen (CAS 025614). The last three lots were cited by WASTE (1940) as *A. hortensis*.

ACKNOWLEDGMENTS

I am grateful to Stella M. Davies, N. J. Evans, and F. Naggs for confirming some of my identifications, and to Alva Day for help in determining the tree ferns from Golden Gate Park. Marjorie Schmelzer contributed samples of *Arion distinctus* from the thriving colony in her garden. Gabriel Roth and Gunder Hefta helped in the field.

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A New Subgenus and a New Species of *Greggelix*

(GASTROPODA: SIGMURETHRA: HELMINTHOGLYPTIDAE)

from the Sierra San Pedro Martir, Baja California, Mexico

BY

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(1 Plate; 2 Text figures)

SEVERAL YEARS AGO, the late Allyn G. Smith, at the California Academy of Sciences, noticed two strange lots of shells collected by John Figg-Hoblyn on 24 and 25 March 1954 (CASIZ 025105 and CASIZ 025106) in Cañon Diablito and Cañon del Diablo, respectively, San Pedro Martir Mountains, Baja California. He tentatively labelled these shells *Sonorelix* sp. and referred them to me for further study. Without reproductive anatomies, however, it was impossible to determine their generic affiliations.

Accordingly, on 16 May 1970, I organized an expedition to the Cañon del Diablo area where John Figg-Hoblyn had collected the shells, for the purpose of obtaining live animals. Because of our unfamiliarity with the area, we mistook Cañon Diablito, which opens at the end of the dirt access road, for Cañon del Diablo, which opens about one mile north of the road, and we collected only in Diablito. Nevertheless, I found one live adult and my colleague, Richard H. Russell, found one live juvenile, which I subsequently raised to adulthood. Both specimens were found to have an anatomy closely resembling that of *Greggelix* W. B. Miller, 1973. One striking feature was the presence of vestigial mucus glands on the vagina, a characteristic that I have observed in only one other helminthoglyptid, namely *Greggelix loehri* (Gabb, 1868) (Miller, 1981: 736, 737).

The shell characters, however, were significantly different from those of the known species of the genus, namely *Greggelix loehri* (Gabb, 1868), *G. indigena* (Mabille, 1895), and *G. punctata* W. B. Miller, 1981. A subgeneric status, in the genus *Greggelix*, appeared indicated for this new species, but the question immediately arose to whether the vestigial mucus glands were an abnormal singularity or a consistent characteristic of the species.

An opportunity for additional collecting did not occur until 15 March 1981 when my colleagues, Noorullah

Babrakzai and Richard L. Reeder, and I made a determined effort to collect a statistically sufficient sample of live animals, from Cañon Diablito as well as from Cañon del Diablo. Two days of arduous digging in rock piles yielded four live adults from Cañon Diablito and eight live adults and two live juveniles from Cañon del Diablo. The 12 adults were dissected and all showed vestigial mucus glands, with ten specimens showing one gland and the other two showing two glands. Accordingly, a new species and a new subgenus can now be described with confidence.

Martirelix W. B. Miller, subgen. nov.

Shell relatively small for the genus, with elevated, broadly-conic spire, relatively narrow umbilicus, and moderately reflected peristome. Reproductive structures generally as in *Greggelix* s.s. but with a verge consisting of a short, cylindrical shaft and a paraboloid tip. Mantle collar and edge of foot with a bright orange mucus.

Type species: *Greggelix (Martirelix) babrakzai* W. B. Miller, spec. nov.

The smaller, more globose, generally higher spired shell is the main differentiating external character of this subgenus. In *Greggelix* s.s., the spire is usually almost flat, the umbilicus is very wide, and the peristome is strongly reflected. In the living animal, the orange mucus of *Martirelix* immediately separates it from *Greggelix* s.s., whose mantle collar and edge of foot have a bright chartreuse to green color. In its anatomy, *Martirelix* has the unusually long spermathecal diverticulum and epiphallic caecum of the genus, although the latter is not quite as long as in *Greggelix*, s.s. Moreover, the verge is short cylindrical, with a paraboloid tip, whereas in *Greggelix* s.s. it is almost perfectly spherical.

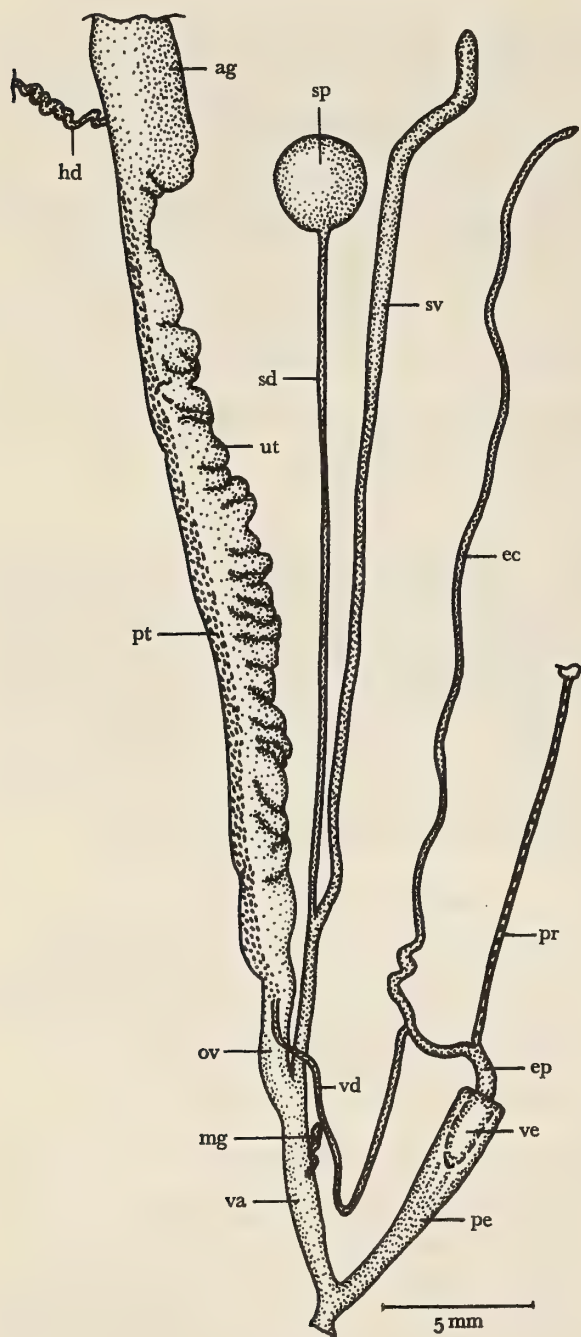


Figure 1

Greggelix (Martirelix) babrakzaii W. B. Miller, spec. nov.

Reproductive system of holotype; ovotestis and part of albumen gland omitted. Drawing made from projection of stained whole mount.

ag—albumen gland; ec—epiphallus caecum; ep—epiphallus; go—genital orifice; hd—hermaphroditic duct; mg—mucus gland; ov—oviduct; pe—penis; pr—penial retractor; pt—prostate; sd—spermathecal duct; sp—spermatheca; sv—spermathecal diverticulum; ut—uterus; va—vagina; vd—vas deferens; ve—verge

Martirelix is currently monotypic. The type species is equipped with one or two vestigial mucus glands attached to the vagina, a character also found in *Greggelix (Greggelix) loehri* but not in *G. (G.) indigena* or *G. (G.) punctata*.

To date, *Martirelix* is known only from Cañon Diablito and Cañon del Diablo, Sierra San Pedro Martir, Baja California. Shells tentatively referable to this subgenus have also been collected in the Sierra la Libertad southwest of Bahía de Los Angeles, some 300 km to the southeast, but specific identification will have to await the availability of live animals.

The name *Martirelix* is feminine. It is a composite formed from the locality name, San Pedro Martir, and the Greek *helix* (coiled, spiral) which has been used repeatedly in malacology to refer to helicoid land snails.

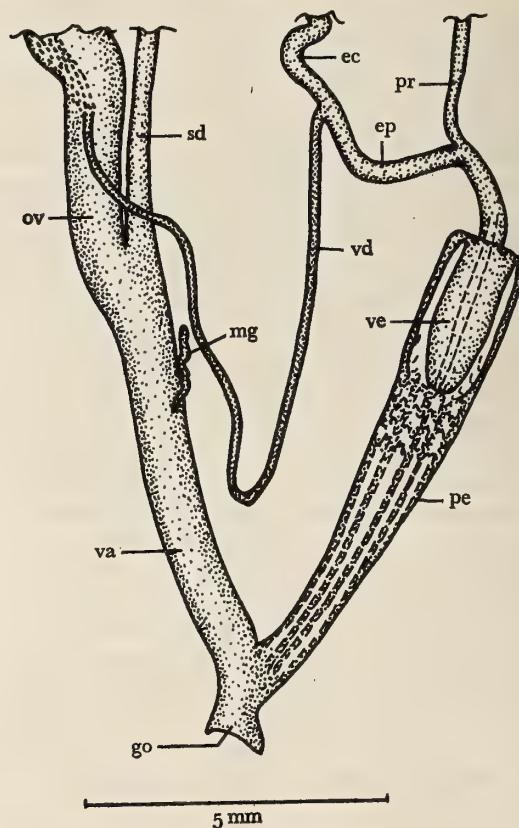


Figure 2

Greggelix (Martirelix) babrakzaii W. B. Miller, spec. nov.

Distal reproductive structures of holotype, showing internal features of penis and relative size and position of mucus gland.

Greggelix (Martirelix) babrakzaii W. B. Miller, spec. nov.

Diagnosis: A small sized, globose *Greggelix* with well-formed umbilicus partly covered by reflected peristome

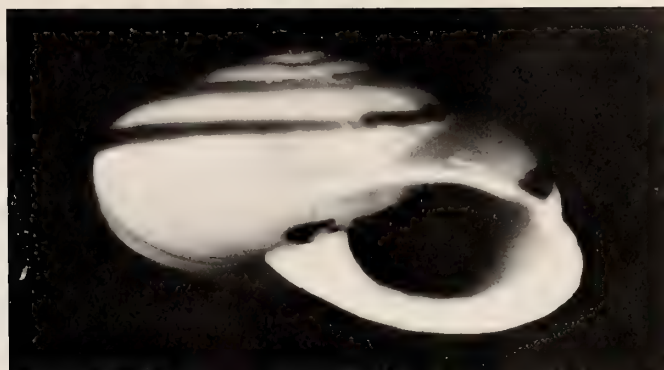


Figure 3



Figure 4



Figure 5

Greggelix (Martirelix) babrakzaii W. B. Miller, spec. nov.

Shell of Holotype, CAS no. 025103; diameter 20.5 mm

Figure 3: Apertural view. Figure 4: Apical view. Figure 5: Umbilical view.

and with a sculpture of radial growth wrinkles covered by a smooth, shiny periostracum; on the last part of body whorl, behind the reflected peristome, numerous, closely-set, raised papillae are superimposed over the growth striae. Genitalia with one or two vestigial mucus glands inserted on the vagina, and with short, cylindrical, paraboloid-tipped verge.

Description of shell of holotype: Shell relatively small for the genus, solid, low conic, helicoid, umbilicate, the umbilicus contained nine times in the diameter. Color light tan with dark chestnut-brown band on the shoulder, bordered above and below by a narrow band slightly lighter than the body of the shell. Embryonic shell of $1\frac{3}{4}$ whorls with fine, closely-set, radial wrinkles superimposed with widely-spaced, punctate papillae. Post-embryonic whorls with coarser growth wrinkles, also superimposed with widely-spaced, punctate papillae for about one and one quarter whorls after which the papillae are absent. The penultimate whorl and most of the body whorl have only radial growth wrinkles and a smooth, shiny periostracum. The last part of the body whorl descends markedly to the aperture and the reflected peristome; in this descending region, numerous, closely-set papillae, varying from punctate to hyphen-shaped, are superimposed over the growth striae. The papillae are also present within the umbilicus. Peristome moderately reflected, the columellar end partly covering the umbilicus. Diameter 20.5mm; height 12.0mm; diameter of umbilicus 2.3mm; number of whorls $4\frac{3}{4}$.

Anatomy of holotype: The principal distinguishing characters are found in the reproductive system which exhibits the general characters of the genus, namely exceptionally long spermathecal diverticulum and epiphallic caecum, no dark apparatus, and a small verge in the saccular penis. The verge, however, is short cylindrical in shape, with a paraboloid tip. The saccular penis has five to six anastomosing, wavy, longitudinal pilasters along the internal wall. A single vestigial mucus gland is inserted on the vagina. The length of the epiphallic caecum is approximately equal to the length of the spermathecal duct. Another anatomical character of diagnostic value is the color of the mucus secretions on the mantle collar and at the edge of the foot and tail which is a bright orange.

Type Locality: Cañon Diablito, East slope of Sierra San Pedro Martir, Baja California, Mexico; ca. 1km up canyon from its mouth, among large granite boulders in decomposing granite, on right bank. Lat. $31^{\circ} 05.1' N$; long. $115^{\circ} 23.5' W$; elev. ca. 700m (reference: Cetenal Carta Topografica H 11B45, San Rafael, Baja California).

Type Material: **Holotype:** California Academy of Sciences no. 025103.

Paratypes: Academy of Natural Sciences, Philadelphia, no. 354221; California Academy of Sciences nos. 025104, 025105, 025106; Field Museum of Natural History no. 206299; U.S. National Museum no. 792374; University of Texas at El Paso no. 8513.

Discussion: The reproductive system of *Greggelix* (*Martirelix*) *babrakzaii* is remarkably similar to that of *Greggelix* (*Greggelix*) *loehri*, which inhabits a restricted area of the Sierra de la Giganta in Arroyo San Javier, some 700km to the southeast. The presence of one or two vestigial mucus glands on the vagina is particularly intriguing. As stated in MILLER (1981: 737), the occurrence of these vestigial mucus glands appears to be evidence that the gene, or genes, for these structures have not been completely eliminated or repressed from the genome. It is interesting to note, however, that *G. (M.) babrakzaii* and *G. (G.) loehri* are the only two dartless helminthoglyptids known to the author that exhibit such vestigial mucus glands. Although the presence of these glands in these two species might tempt one to infer an especially close relationship, the similar shell characters of *G. (G.) loehri*, *G. (G.) indigena*, and *G. (G.) punctata*, as well as their chartreuse colored mantle collar, their spherical verge, and their geographical proximity clearly link them more closely, evolutionarily, to each other than to *G. (M.) babrakzaii*. Instead, it can be hypothesized that when the ancestral *Greggelix* founder speciated from a helminthoglyptid fully equipped with dart apparatus and mucus glands, the genes responsible for developing the mucus glands were not completely eliminated from the genome but instead were more or less repressed; in *G. (G.) loehri* and *G. (M.) babrakzaii*, they have been partly de-repressed. It will be interesting to note whether these genes will be found to be expressed in any other populations or new species yet to be discovered.

Variations in the paratypes: Bleached shells were abundantly scattered on the ground in the vicinity of rock formations. Live animals, however, were scarce and could be obtained only after much arduous digging. A total of 162 adult shells were collected in the type lot from Cañon Diablito in May 1970 and in March 1981. The largest shell measures 22.0mm in diameter while the smallest measures 17.4mm. All have a low conic spire, relatively narrow umbilicus, and a moderately reflected peristome; when not excessively worn, they also show the granular, papillate sculpture on the last part of the body whorl, just behind the peristome. Shells from Cañon del Diablo, not considered to be in the type population, tend to be slightly smaller and more globose than shells from Cañon Diablito. It must be pointed out, however, that all of these shells, some 79 specimens, were obtained from one single, isolated population, in a narrow granitic ravine about 1km up-

stream from the mouth of the canyon.

A total of 14 adults were dissected. Twelve of them, including the holotype, had only one mucus gland, inserted on the vagina, and the other two had two such glands. When two glands are present, their ducts insert separately on the vagina approximately on opposite sides from each other.

Distribution and Habitat: *Greggelix (Martirelix) babrakzai* is known only from Cañon Diablito and Cañon del Diablo. It is reasonable to assume, however, that it occurs in other canyons on the east slope of the Sierra San Pedro Martir, especially the deeper canyons to the south such as Cañon Providencia, Cañon El Cajon, and Cañon Agua Caliente. Its possible occurrence in the mountains south of Bahia de los Angeles remains to be confirmed. *G. (M.) babrakzai* inhabits rock piles and crevices in ravines and outcrops on the canyon slopes above the streambed. The vegetation is typical of the Lower Sonoran life zone, most notably mesquite (*Prosopis glandulosa*), ironwood (*Olneya tesota*), cat's claw (*Acacia greggi*), palo verde (*Cercidium microphyllum*), cardon (*Pachycereus pringlei*), senita (*Lophocereus schotti*), cholla (*Opuntia cholla*), ocotillo (*Fouquieria splendens*), chuparosa (*Beloperone californica*), agave (*Agave deserti*), and nolina (*Nolina parryi*).

Etymology: This species is named after Noorullah Babrakzai, friend and colleague, who has accompanied and encouraged me on many expeditions, including the one to Cañon del Diablo where he uncovered a "jackpot" of live adults.

ACKNOWLEDGMENTS

I wish to express my gratitude to my former colleague, Richard H. Russell, who assisted me in my first expedition to Cañon Diablito, and to my former graduate students and colleagues, Noorullah Babrakzai and Richard L. Reeder, who assisted me in my second expedition to Cañon Diablito and Cañon del Diablo. I wish to thank Noorullah Babrakzai for the photographs of the holotype, and Carl C. Christensen and Barry Roth for reading and criticizing this manuscript.

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(October 1981)

An Incident of Predation by the Loco
Concholepas concholepas Bruguière, 1789
on the Red Abalone *Haliotis rufescens* Swainson, 1822
in a Chilean Laboratory

BY

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(1 Plate)

INTRODUCTION

THE CHILEAN LOCO *Concholepas concholepas* is a muricid occupying the western South American sublittoral from Cape Horn to Central Peru. This is the last surviving species of a genus whose other representatives appear only in Pleistocene and older fossil records (STUARDO, 1979), and is found from lower low tide marks to a depth of 30m. It feeds primarily on barnacles, although its diet may include limpets, mussels, and tunicates (CASTILLA, *et al.*, 1979). In the laboratory it will accept a variety of invertebrate tissue. The main limiting factor on loco population growth is commercial fishing, as locos are an esteemed food item in Chile. The total catch in shell for 1977 exceeded 11000 tons (LORENZEN *et al.*, 1979). The California red abalone *Haliotis rufescens* is an herbivore, occupying habitats similar to those of locos. It prefers areas with less violent wave action and positions advantageous for capturing and feeding upon pieces of drift kelp. *Haliotis rufescens* and other *Haliotis* species are commercialized in California in a manner analogous to the loco in Chile.

This note describes a laboratory observation made on predation by locos upon abalones under fortuitous circumstances at the Centro de Investigaciones Submarinas (CIS), Universidad del Norte, Coquimbo, Chile. Some research has been carried out at this laboratory on the feasibility of introducing the red abalone to suitable Chilean coastal habitats as a new marine resource (EBERT, 1979).

METHODS AND RESULTS

Over 300 hatchery reared *Haliotis rufescens* from California have been maintained at CIS since September, 1979, in laboratory aquaria provided with continuously exchanged seawater. These abalone have survived and grown well,

feeding on the brown alga *Lessonia flavicans* provided as forage. They move about their holding tanks with tentacles extended, particularly at night, and show normal behavioral patterns such as capture of algal fragments with the leading shell edge.

Eight of these abalone, ranging in length from 10 to 14cm were placed in equal numbers in two holding cages at 10m depth on the bottom of Herradura Bay next to a rocky underwater outcrop not far from the laboratory. This was the first test in which the abalone were exposed to field conditions in Chile after initial studies had been carried out in laboratory tanks (EBERT, 1979). The circular cages were approximately 0.8m in diameter and 0.5m in height and constructed of steel reinforcing bar covered with 2cm mesh galvanized iron screening. The cages were fitted with asbestos composition floors, with an asbestos plate arranged at a 45° angle with the floor, providing a "crevice" into which the abalone could retreat. These abalone were visited approximately every three days, using SCUBA, for two months between December 1979 and February 1980. Dives were made at various times of the day, and included two midnight dives. During the dives, abalone were observed, potential predators were removed from surfaces of the cages, and fronds of *Lessonia* growing nearby were routinely provided as forage.

Throughout the two months of underwater observation, it became evident that although the abalone were feeding on the algae presented to them, their behavior became increasingly conservative until they were constantly seen to be in retracted, defensive positions and showed apparently no change in position from visit to visit. Upon close observation of the animals it was discovered that some showed damaged or missing tentacles, and scarred epipodial surfaces. Four abalone were immediately removed from one cage and returned to the laboratory for observation and recuperation under protected conditions. Figure 1 demonstrates this tentacle damage.

Since previous laboratory experimentation carried out with these abalone had not shown them to be attractive to the predatory *Concholepas* (EBERT, 1979), the four abalone were placed in a 500 L aquarium which was also used as a holding tank for about 10 adult locos. Upon our return to the laboratory after 16 hours (overnight) it was observed that two locos were in the process of consuming one abalone and a single loco was consuming another. Two remaining abalone were untouched, although in defensive positions, with other locos nearby. The prey abalone were weakly attached to the sides of the aquarium, with attacking locos affixed atop their shells, their heads extended downward while feeding on tissues dorsal to the abalone head or epipodium (Figure 2). The animals were quickly separated, but the abalone, which were moribund, and had sustained several wounds each, ceased to show any signs of life within a few minutes of separation. The two unmolested abalone were intact except for existing tentacle damage. These abalone, plus the additional four recovered from the second cage, were placed in a separate aquarium, and required 24-48 h before they assumed non-defensive postures and began active feeding. Damaged tentacles were regenerated within 2-4 weeks.

DISCUSSION AND CONCLUSIONS

Since there was no danger from large predators such as crabs and starfish that had shown potential for attacking the abalone under laboratory conditions (EBERT, 1979), it was assumed that small organisms able to pass the 2 cm mesh of the cages were responsible for minor injuries and defensive posturing of the abalone. The two most likely candidates observed during diving were the rock shrimp *Rhyncocinetes typus* Milne-Edwards, 1844, and juveniles of the kyphosid fish *Doidixodon laevis* Tschudi, 1844. These organisms were seen to enter abalone crevices on various occasions during our underwater observation but visibility and time constraints prevented detailed observation of their activity. Within the laboratory it had been previously demonstrated that *Doidixodon* attacked abalone tentacles (EBERT, 1979), although the rock shrimp apparently did not. Abalone inhabiting community aquaria which contain a diversity of local organisms exclusive of *Doidixodon* have survived well for over 18 months, showing normal behavior and normal tentacles.

I therefore hypothesize that abalone placed in the field must be weakened by the presence of one or more sublethal attackers that may then render them susceptible to lethal predatory attack by locos as witnessed in the laboratory. The observation was carried out under artificial conditions imposed by caging, and in the protected environment which cannot be considered a prime abalone habitat.

Introduction of any species into a new environment raises a cloud of questions, if not a storm of ecological controversy much too diverse to discuss here. Questions of whether *Haliotis* will damage the Chilean environment, or *vice versa*, are overshadowed by the great theoretical problem of why there are no indigenous haliotid species known from Chile. Although at this writing, research on problems of introduction of *H. rufescens* have been suspended pending approval of new programs, we hope to place about 5000 small male *H. rufescens* on an isolated rocky outcrop which appears favorable for their survival. These animals, produced from the first spawning of *H. rufescens* in the southern hemisphere (B. Owen, unpub.) have shown excellent growth in our laboratory after a two year period. The ultimate decision as to whether or not *H. rufescens* can survive in the Chilean inshore ecosystem will be based in great part on results of such field testing.

ACKNOWLEDGMENTS

This work was supported by the Organization of American States performance contract No. 2981 to Dr. C. A. Viviani (CIS) and E. E. Ebert acting as private consultant. I thank Earl E. Ebert for design of the underwater cages, and for his suggestions regarding handling of the abalone.

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Figure Legends

Figure 1

Pedal aspect of *H. rufescens* photographed through aquarium glass. Epipodial tentacles show stubby appearance due to attack by as yet unspecified organisms. Tentacles are normally about 1/3 longer with pointed tips.

Figure 2

Wound (arrow) produced dorsal to head region of *H. rufescens* killed by *C. concholepas*. Other wounds similar to this occurred laterally, all penetrating to the coelomic cavity.

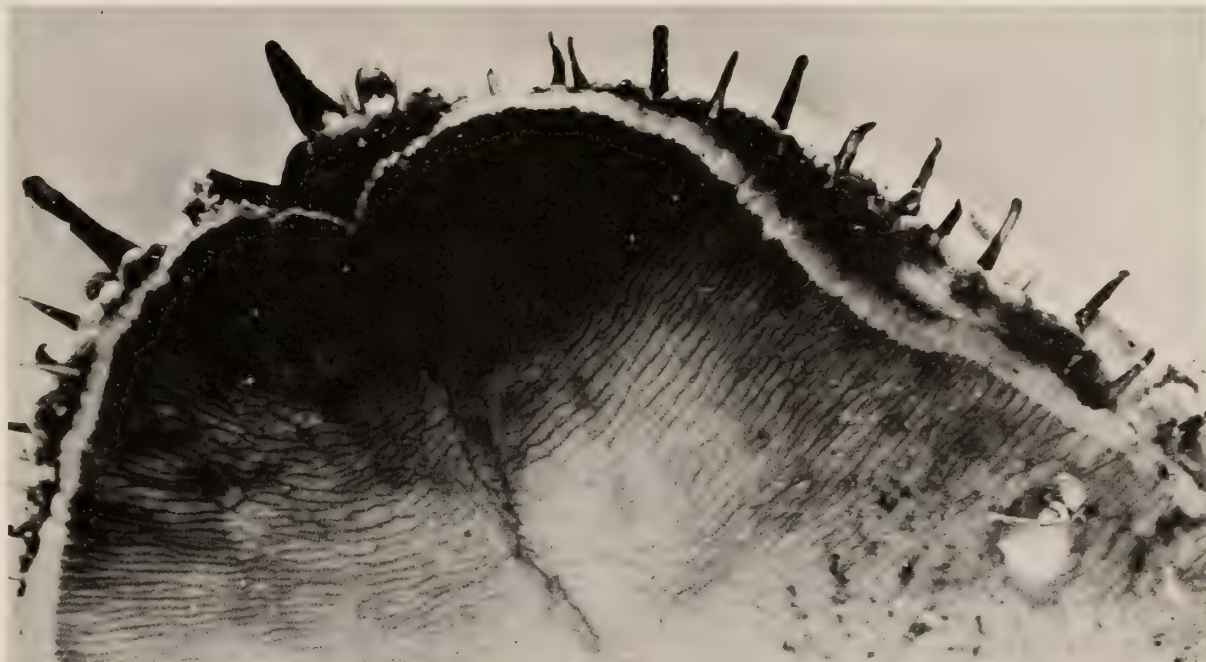


Figure 1



Figure 2

Molluscan Distributional Records from the Cumberland River, Kentucky

BY

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INTRODUCTION

IN AN ATTEMPT to upgrade the distributional knowledge in Kentucky aquatic organisms, which is sorely lacking in many taxa (BRANSON, *et al.*, 1981), we have recently initiated a series of stream inventories for gastropods (BRANSON & BATCH, 1982, 1982a). This contribution extends the observations to 45 collecting sites in the Cumberland River system.

COLLECTING SITES

The collecting stations delineated below are numbered consecutively, and in the annotated list that follows species and specimens are assigned to the stations by number. The figures in parentheses represent the number of specimens collected.

1. 19 September 1978. Woodland pond, 100m north of junction of U.S. routes 25W and 25E, Laurel County.
2. 6 May 1970. Rockcastle River at Kentucky Route 80, Laurel County.
3. 20 July 1968. Cumberland River at Kentucky Route 896, McCreary County.
4. 19 July 1968. Rockcastle River at Livingston, Rockcastle River.
5. 23 April 1978. Rockcastle River at Kentucky Route 490, Rockcastle-Laurel county line.
6. 19 July 1980. Buck Creek, Kentucky State Route 192, Pulaski County.
7. 27 June 1967. Mouth of Hammonds Fork of Clear Creek, Rockcastle County.
8. 11 July 1967. Clear Creek at Wildie, Rockcastle County.
9. 2 October 1970. Horse Lick Creek at Jackson-Rockcastle county line.
10. 18 May 1970. Rock Creek, just above mouth on South Fork of the Cumberland River, McCreary County.
11. 8 May 1966. Clear Creek, 4.6km SE of Disputanta, Mount Vernon Road, Rockcastle County.
12. 24 July 1975. Pitman Creek at Somerset, Pulaski County.
13. 7 May 1967. Mill Creek, Kentucky Route 221, Bell County.
14. 5 September 1980. Rockcastle River just below the narrows, Laurel County.
15. 10 September 1980. Pond just below main entrance to Pine Mountain State Park, Bell County.
16. 12 October 1980. Cumberland River at River Mile 652.5, near Barbourville, Knox County.
17. 5 July 1980. Roundstone Creek, U.S. Route 25, Rockcastle County.
18. 25 July 1979. Spring on Dry Fork of Skeggs Creek, Kentucky Route 1249, Rockcastle County.
19. 9 December 1980. Richland Creek, 1.4km above mouth, Bell County.
20. 10 December 1980. Cumberland River at River Mile 635, Knox County.
21. 9 December 1980. Cumberland River at River Mile 631.5, Knox County.
22. 9 December 1980. Cumberland River at River Mile 629.5, Knox County.
23. 8 December 1980. Cumberland River at River Mile 633, Knox County.
24. 5 September 1980. Rockcastle River at Billows, Rockcastle County.
25. 9 May 1980. Buck Creek, Kentucky Route 1677, Pulaski County.
26. 10 September 1980. Clear Creek at Pineville, Bell County.
27. 10 September 1980. Clear Creek at Pineville, Bell County.
28. 13 September 1980. Spring at base of Black Mountain, State Route 38, Harlan County.
29. 11 September 1980. Small unnamed tributary of Pitman Creek, 1.3km north of Somerset, Pulaski County.
30. 1 August 1980. Mouth of Brushy Creek, McCreary County.
31. 20 November 1980. Whorry Bog, 0.3km north of Tennessee State line, U.S. Route 27, McCreary County.
32. 10 September 1980. Farm pond at Whitley City, McCreary County.
33. 25 November 1980. Roadside ditch, 2.8km north of Tennessee State line, U.S. Route 27, McCreary County.
34. 11 October 1980. Ritner Ford, Little South Fork of the Cumberland River, McCreary County.
35. 9 May 1980. Rockcastle River at Interstate 75 crossing, Rockcastle County.
36. 14 September 1980. Little South Fork of the Cumberland River, State Route 80 crossing, McCreary County.
37. 17 September 1980. Indian Creek at State Route 700 crossing, McCreary County.
38. 10 October 1980. Little South Fork of the Cumberland River at river mile 10.6, McCreary County.
39. 10 October 1980. Little South Fork of the Cumberland River, State Route 92, McCreary County.
40. 10 October 1980. Little South Fork of the Cumberland River at mouth of Corder Creek, McCreary County.

41. 10 October 1980. Little South Fork of the Cumberland River at river mile 7.9, McCreary County.
42. 10 October 1980. Little South Fork of the Cumberland River at river mile 5.4, McCreary County.
43. 10 October 1980. Little South Fork of the Cumberland River at river mile 12.5, McCreary County.
44. 11 October 1980. Little South Fork of the Cumberland River at river mile 10.6, McCreary County.
45. 11 October 1980. Little South Fork of the Cumberland River at State Route 92 crossing, McCreary County.

ANNOTATED LIST

SPHAERIACEA

CORBICULIDAE

Corbicula manilensis (Philippi, 1844)

Collecting site: 4 (8).

Often a noxious pest, and possibly an aggressive competitor with native sphaeriids and unionids, this clam is seasonally abundant in the Rockcastle River. It has nearly excluded sphaeriids from many sites in the Little South Fork of the Cumberland, where it is exceptionally abundant (BRANSON & BATCH, 1982), particularly in the scenic section of the stream between State Route 80 and the mouth in McCreary County.

SPHAERIIDAE

Sphaerium striatinum (Lamarck, 1818)

Collecting sites: 12 (9), 19 (6).

Nearly universally distributed in small rivers and creeks in Kentucky.

Pegias fabula (Lea, 1831).

Collecting site: 9 (2).

Pegias was reported from this site by BLANKENSHIP (1971) and by STARNES & STARNES (1980). We observed the species on nine different riffles in the Little South Fork of the Cumberland River but did not collect specimens, since this clam is considered as endangered in Kentucky (BRANSON *et al.*, 1981). STARNES & STARNES' (1980) suggestion that the species should be listed as threatened rather than endangered is rejected, since the Little South Fork of the Cumberland population is the only site known at present which is not heavily impacted by human activities in Kentucky. Furthermore, mining operations are underway near that drainage, silt already being obvious in many of the pools and backwaters. Furthermore, the population of *Corbicula* in the stream is very large, doubtless creating competition problems for the native species.

PLEUROCERIDAE

Many of the putative pleurocerid species continue to cause problems for biologists with regard to diagnosis. The

faunas of the Green and Cumberland rivers of Kentucky and Tennessee include several of these species, some of which seem to have been described and named simply because they occurred in drainages other than those investigated at earlier dates. For example, *Goniobasis semicarinata* is relatively common in many Cumberland tributaries but most writers have not reported the species from that drainage, possibly because CALVIN GOODRICH (1940) listed the range of the species as "tributaries of the Ohio River, Sciota River, Ohio, to Big Blue River, Indiana; Licking River to Salt River in Kentucky; two creeks of Green River of Kentucky."

Many specimens from the Little South Fork of the Cumberland and other tributaries of the Big South Fork drainage are nearly indistinguishable from members of the *Goniobasis* (*Mudalia*) *potosiensis* (Lea, 1841)-*G. livescens* (Menke, 1830) complex (Carol B. Stein, Ohio State University, personal communication).

Anculosa praerosa (Say, 1824)

Collecting sites: 2 (2), 6 (2), 24 (6), and Smith Fork River, 7 km south of Lancaster, Smith County, Tennessee (2) (14 June 1974).

The two specimens from Station 2 are very similar to those reported from the Cumberland River in Russell County, Kentucky by GOODRICH (1934) as *Anculosa subglobosa* (Say, 1825), being very low of spire. The species is listed as Threatened in Kentucky (BRANSON *et al.*, 1981) and is currently under review for federal listing (Federal Register 1980).

Goniobasis laqueata (Say, 1829)

Collecting sites: 5 (5), 17 (2), 38 (4), 39 (28), 41 (9), 42 (104), 43 (1).

Carol Stein kindly compared samples from the Little South Fork of the Cumberland River with ones in the Ohio State University Museum, concluding that they seemed to be intermediate between typical *Goniobasis laqueata* and *G. edgariana* (Lea, 1841).

Goniobasis cf. livescens (Menke, 1830)

Collecting sites: 2 (9), 4 (30), 6 (16), 10 (3), 11 (55), 12 (3), 13 (23), 19 (3), 40 (28).

Discussed above. These specimens were diagnosed as *G. ebenum* (Lea) by Dr. George Davis, Academy of Natural Sciences of Philadelphia.

Goniobasis plicata-striata Wetherby, 1876

Collecting sites: 7 (31), 18 (10).

This may be a costulate form of *Goniobasis laqueata*, similar to the nominate *G. laqueata costulata* (Lea, 1841) from the Green River in Kentucky and Duck River in Tennessee.

Goniobasis semicarinata (Say, 1829)

Collecting sites: 8 (4), 12 (15), 19 (15), 22 (8), 37 (4), 40 (300), 41 (50), 42 (250), 44 (50), 45 (50).

Other than being encrusted with a black substance which often obscures the true shell color (horn to dark horn) and

sculpturing, these specimens are indistinguishable from *Goniobasis semicarinata* from the Licking and Kentucky rivers.

Lithasia armigera (Say, 1821)

Collecting site: 3 (1).

A rare and endangered species in Kentucky (BRANSON *et al.*, 1981) and elsewhere (Federal Register 1980).

Lithasia obovata (Say, 1829)

Collecting sites: 4 (1), 35 (2).

Listed as of Special Concern in Kentucky (BRANSON *et al.*, 1981), this species is very rare in the Cumberland River drainage.

Pleurocera canaliculatum (Say, 1821)

Collecting sites: 4 (15), 36 (1), and Center Hill Reservoir, Dekalb County, Tennessee (2) (19 June 1974).

Recent collecting indicates that this species is more common in portions of the Kentucky and Green river basins than in the Cumberland.

Pleurocera curta (Haldeman, 1841)

Collecting sites: 2 (8), 3 (4).

Of Special Concern in Kentucky (Branson *et al.*, 1981), this low-spined snail has become much less abundant in the Cumberland River with increased mining activities.

VIVIPARIDAE

Lioplax subcarinata occidentalis (Pilsbry, 1935)

Collecting site: 3 (4).

Campeloma crassula Rafinesque, 1819

Collecting sites: 27 (1), 34 (10).

Campeloma integrum (Say, 1821)

Collecting sites: 19 (7), 32 (6).

Campeloma rufum (Haldeman, 1841)

Collecting site: 25 (1).

Viviparus gorgianus Lea, 1834

Collecting site: 2 (1).

This species heretofore was known only from two Kentucky sites, Kenton (Licking River) and Warren (Green River) counties.

ANCYLOPLANORBIDAE

HUBENDICK (1978) recently offered a revisional version of the families Bulinidae, Planorbidae, and Ancyliidae, combining under the single epithet, Ancyloplanorbidae. He also combined *Menetus* and *Promenetus* with *Planorbula*, the last having priority, and *Armiger* was combined with *Gyraulus*. We follow his rationale here.

Ferrissa rivularis (Say, 1819)

Collecting sites: 20 (10), 23 (4).

Ancyliids are often overlooked in general collecting because of their small size and habitat. Thus, the family is very poorly known in Kentucky.

Gyraulus parvus (Say, 1817)

Collecting site: 15 (12).

Distributional records for all the small planorb snails in Kentucky are very scarce, for the reason mentioned above.

Planorbula (Menetus) sampsoni (Ancey, 1885)

Collecting sites: 16 (1), 23 (7).

The specimens were removed from dead leaves in backwater situations. The only previous record for this species in Kentucky came from a small woodland pond in Pine Mountain State Park in Bell county (BRANSON, 1972).

Helisoma anceps (Menke, 1830)

Collecting sites: 1 (7), 14 (2), 19 (6), 27 (1), 30 (1), 31 (7).

Nearly ubiquitously distributed in the Cumberland Plateau, Escarpment, and Cumberland River Enclave, this species is apparently more abundant in upland habitats than the next.

Helisoma trivolvis (Say, 1817)

Collecting site: 4 (1).

LYMNAEIDAE

Lymnaea columella Say, 1817

Collecting sites: 15 (8), 24 (1), 31 (7), 33 (1).

PHYSIDAE

Because of the chaotic state of systematic knowledge in this family, any specific diagnoses based upon shell characters are by necessity tentative, as are the ones discussed here.

Physa heterostropha (Say, 1817)

Collecting site: 15 (6).

Physa integra (Haldeman, 1841)

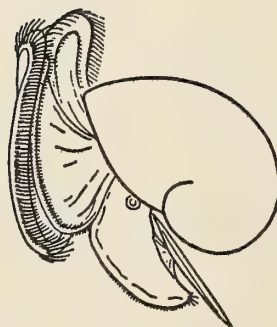
Collecting sites: 19 (8), 20 (13), 21 (11), 22 (16), 23 (7), 26 (15), 28 (11), 29 (20).

ACKNOWLEDGEMENTS

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Studies on the Reproductive Biology
of Some Prosobranchs from the Coast of Karachi (Pakistan)
Bordering the Northern Arabian Sea.
I. Observations on *Planaxis sulcatus* (Born, 1780).

BY

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(1 Text figure)

INTRODUCTION

THE BREEDING HABITS of the members of the superfamily Cerithiacea (including Planaxidae) have been studied in the past by a number of workers: BANDEL (1976), CANNON (1975), D'ASARO (1970), DAVIS (1967), DESAI (1962), HABE (1960), HOUBRICK (1971, 1973), LEBOUR (1937, 1945), NATARAJAN (1957), PILKINGTON (1974), RAMAMOORTHY & NATARAJAN (1973), WOLFSON (1969), YAMADA & SANKURATHRI (1977). Three types of larval development (see Thorson, 1946) are shown by members of this superfamily. It is interesting to note that only two species of cerithiaceans are so far reported to be viviparous and both of them belong to the family Planaxidae. These are, *Planaxis sulcatus* from the Persian Gulf (THORSON, 1940) and *P. nucleus* from the Caribbean (BANDEL, 1976). The other members of the superfamily either exhibit pelagic larval development or direct development from benthonic egg capsules. *Planaxis sulcatus* from New Caledonia is also known to hatch as small veligers (RISBEC, 1935 cited in BANDEL, 1976). *Planaxis lineatus*, another species from the Caribbean, was stated by RISBEC (1935) to show pelagic larval development.

Nothing is known about the breeding habits of the members of Planaxidae of the northern Arabian Sea. The present paper describes the breeding habits and development of early juvenile shell of *Planaxis sulcatus* from the Karachi coast.

METHODS

Specimens of *Planaxis sulcatus* were collected bimonthly from the rocky shore of Buleji and occasionally from

Keamari backwaters, Manora, Paradise Point and Cape Monze. They were maintained in the laboratory in glass bowls of 300 ml capacity. One specimen was placed in one bowl in order to determine the number of juveniles per individual. The newly hatched juveniles were transferred to separate glass bowls containing fresh aerated sea water. No food was provided to the juveniles so hatched. Dimensions of juvenile shells were measured at various stages with an ocular micrometer on a stereoscopic microscope. Illustrations were prepared with a camera lucida.

OBSERVATIONS

Planaxis sulcatus occurs abundantly in the upper littoral zone of the rocky shore of Buleji at a tidal height of 2-3 m. Observations were made mainly on the specimens collected from this site. The embryonic development of this species up to the hatching stage, within the maternal body, was not investigated, and observations recorded here relate to the stage just after hatching. In this species all the developmental stages are passed within the maternal body and the embryos are retained in the pallial duct until they reach the crawling stage, at which they hatch.

Breeding Season: Miniature snails hatched in the laboratory from January to August with a peak in June and July. Almost every specimen of the July sample produced miniature snails. Specimens from Keamari sea-wall and Cape Monze also hatched in the laboratory in July 1976 and January 1977, respectively. No hatching was recorded from September to December although specimens were placed for hatching during this period.

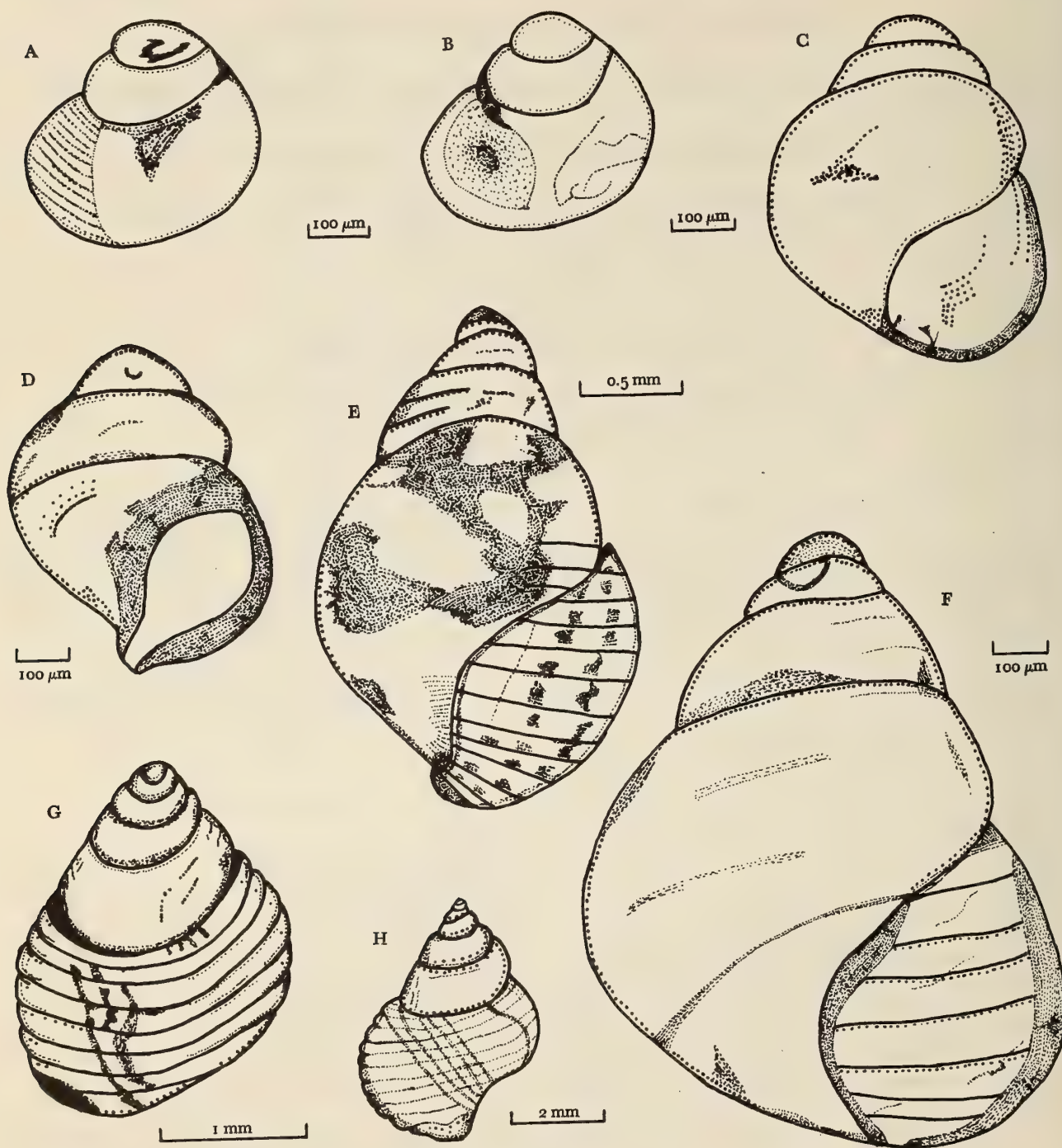


Figure 1

Planaxis sulcatus. A. dorsal view of newly hatched fry; B. dorsal view of same, showing aperture of the shell; C. ventral view of 96 hrs fry; D. ventral view of 48 hrs old juveniles; E. ventral view of one and a half month old juvenile; F. ventral view of 480 hrs fry; G. dorsal view of two months and six days juvenile; H. dorsal view of seven months juvenile.

Brood Size: The number of juveniles hatched per snail varied from 167 to 596 with an average of 328. This wide range may be attributable to the reason that the specimens used were probably already in the process of hatching when collected. The mother specimens did not differ much in size (17.3 to 19.6 mm in height and 10.9 to 12.3 mm in width); thus the differences in the brood size may not be attributable to the size of the parent snails.

Shell Growth: At hatching the juvenile shell (Figures 1 A & B) is transparent and light brown in colour, has two and a half whorls and averages 376 μm in height (range: 353 to 388 μm). Incipient spiral ribs are present on the body whorl. The shell is sculptureless at this stage and the operculum is hard and dark brownish. Soon after hatching the young snails start crawling over the glass bottom with a well developed foot, which is provided with long tentacles having eyes at their base. Ultimately they reach the water surface and attach themselves just above the water level.

The juveniles thrived well for over seven months after hatching in the laboratory. Measurements of their shell growth and changes in whorl numbers are given in Table 1. After 24 hours of hatching, the spiral ribs became prominent, sutures between the whorls were also well defined and sculpturing on the body whorl was visible. Sculpturing

DISCUSSION

Ovoviviparity is a rare phenomenon in prosobranch gastropods (ANDERSON, 1960; WEBBER, 1977). It is a type of development in which eggs are retained within a brood chamber (pallial oviduct) until they are ready to hatch. Examples of ovoviviparous prosobranchs are *Planaxis sulcatus* (THORSON, 1940), *Thais haemostoma* and *Littorina saxatilis* (LINKE, 1934 cited in ANDERSON, 1960), *Littorina angulifera* (LEBOUR, 1945), *Littorina scabra* (STRUHSAKER, 1966, KOJIMA, 1960), *Acmaea rubella* (THORSON, 1944) and *Nassarius albus* (CATHER, 1973). Two types of ovoviviparity are known; in one the young are born as planktonic veligers for pelagic existence, whereas in the other they are born at a crawling stage for benthic existence. There are, however, instances of species which develop with pelagic larvae in one locality and with non-pelagic larvae feeding on nurse eggs in another locality. Out of the seven species mentioned above, four species, *P. sulcatus*, *L. angulifera*, *T. haemastoma* and *L. scabra* develop differently in different localities (THORSON, 1950; MILEIKOVSKY, 1975). The remaining three species, namely, *L. saxatilis*, *N. albus* and *A. rubella* have been examined from one or two localities only (see THORSON, 1935; CATHER, 1973; MILEIKOVSKY, 1975). Hence nothing could be said about these species whether they exhibit more than one kind of development.

Table 1

The number of whorls and dimensions of shells of the juveniles of *Planaxis sulcatus* at various stages of growth.

	At hatching	12 hrs.	24 hrs.	48 hrs.	480 hrs.	2 months	7 months
Av. no. whorls	2½	3	3 - 4	4	5	6	7
Av. shell height μm	376	410	449	509	1007	2990	5360
Range shell height μm	353 - 368	342 - 547	384 - 576	502 - 596	1003 - 1010	2700 - 3210	4560 - 5480

of the body whorl became more prominent after 48 hours. The shell still had four whorls but grew in thickness. The fifth whorl was added to the shell 15 to 20 days after hatching (Figure 2 F). At this stage growth lines and sutures were well defined, axial ribs were evident and the colour of the shell turned darker. The six-whorls stage was reached in about two months time when the shell acquired thick walls, big body whorls, and a conical spire (Figure 1 G). Growth seemed to decrease from here onwards as the seventh whorl was added after another five months or so. The seven-whorl snails had somewhat rough outer surfaces and thick shell walls.

Specimens from Cape Monze and Keamari sea-wall also hatched in the laboratory. Slight variations in the growth rate of young snails belonging to different populations were noted but these did not differ significantly from those of the Buleji population.

Planaxis sulcatus has also been described to hatch as crawling young in the Persian Gulf by THORSON (1940), who stated that the embryos break out of the egg membrane but remain in the uterus where they feed on other developing eggs and finally emerge as crawling young snails at a much greater size. Growth rates of juveniles after hatching have not been studied earlier in any ovoviviparous prosobranch. The results of the present study show that the juveniles of *P. sulcatus* measure on the average 376 μm on hatching and have two and a half whorls. They become 5 mm high after a growth of seven months acquiring seven whorls. The adults of this species normally show seven to eight whorls. Therefore, the snails reared in the laboratory had almost reached the adult stage. The young snails displayed a rapid growth rate and they would have grown much faster had they been provided with food.

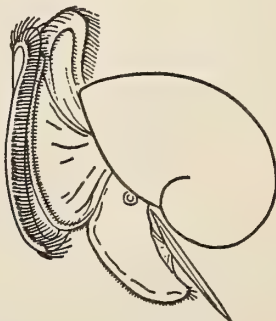
The number of juveniles spawned during this study by *Planaxis sulcatus* varied from 167 to 596, which seems to be a high count compared to other viviparous species, for instance *Littorina saxatilis*, which was reported to have only 28 to 37 eggs inside the body (LEBOUR, 1937). Comparable counts on any other species of *Planaxis* are not available.

SUMMARY

The prosobranch gastropod *Planaxis sulcatus* breeds from January to August on the coast of Karachi in the northern Arabian Sea. It is viviparous. The number of juveniles released per individual varies from 167 to 596. The juveniles at hatching measure on the average 376 μm and their shells have two and a half whorls. They measure five millimeters in height after a growth of seven months in the laboratory.

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Sakuraeolis enosimensis (Baba, 1930)

(Nudibranchia : Aeolidacea)

in San Francisco Bay

BY

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(5 Text figures)

THE AEOLID NUDIBRANCH, *Sakuraeolis enosimensis* (Baba, 1930) has been observed to occur seasonally in San Francisco Bay (Lat. 37° 30' 02" N; Long. 122° 13' 23" W). First collected from the Bay in February 1972, it was misidentified by BEHRENS & TUEL (1977) as a color variation of *Hermisenda crassicornis* (Eschscholtz, 1831). Preserved specimens and color photographs of living specimens were sent to Dr. Kikutarô Baba, who confirmed the identification as *S. enosimensis*.

Sakuraeolis enosimensis is a common inhabitant of the boat floats at Pete's Harbor in the Port of Redwood City, San Francisco Bay, late summer through spring. Peak abundances have been observed in November-December. Its numbers seem to have increased over the years. No particular food substrate has been identified; however, most specimens were collected on or near colonies of the bryozoan *Bugula neritina* Linnaeus, 1758 and the hydrozoans *Obelia* sp. and *Tubularia crocea* (Agassiz, 1862).

Sakuraeolis enosimensis is currently reported by BABA & HAMATANI (1965) to occur on the Pacific Coast side of Japan (Mutsu Bay, Sagami Bay, Suruga Bay, Shima, Seto, Kii, Osaka Bay, Inland Sea of Seto, Saeki Bay, Amakusa) and on the Japan Sea side (Sado Island, Toyama Bay and vicinity). This is the first recorded occurrence of *S. enosimensis* in eastern Pacific waters.

The genus *Sakuraeolis* (type: *Hervia enosimensis* Baba 1930) was recently reviewed and three species added by RUDMAN (1980). 'Sakura' is the native name of the cherry in Japan (BABA & HAMATANI, 1965). The derivation of the trivial name of the type species *enosimensis* is after Enosima, Sagami Bay, Japan the type locality (BABA, 1930).

A brief description of the eastern Pacific specimens is presented here to supplement the original description and alert local workers to this species' characteristics.

External Morphology: The animals are large, up to 40 mm. Cerata are long, up to ½ the body length, numerous, and

densely set. Oral tentacles are long and tapering. Anterior edges of the foot are produced into long tapering foot corners. The tail is long and tapered. The rhinophores are simple and about one-half the length of the oral tentacles (Figure 1).

The cerata are arranged on 6-8 slightly raised arch-shaped pads. The first arch contains 3 rows of cerata on its anterior limb and 2 rows on the posterior limb (Figure 2). Of the remaining ceratal pads posterior to the pericardium, all but the last 2-3 are arch-shaped with a single or double row of cerata. The last couple of pads consist of simple groups. An example of the branchial formula was I 66, II 42, III 30, IV 23, V 17, VI-VIII 2-6.

The genital orifice lies below the anterior limb of the second ceratal pad. A series of fleshy cushions occur on the right margin only of the notum, one lying between each ceratal pad of the left posterior liver. This character first mentioned in BABA (1937:329), is an important discriminant. The three *Sakuraeolids* described by Rudman do not have this unique character (RUDMAN, 1980 and personal communication).

Color: The wide variation in color reported by BABA & HAMATANI (1965) may be observed here also. The body was translucent yellow. Yellow-orange pigment became intense on the head and over the pericardium of some specimens. The color of the liver diverticula demonstrated the greatest variation, ranging from yellow-orange through reddish-brown and in occasional specimens, green. The hue usually intensified toward the distal end of the vein. The rhinophores and cerata are tipped with white. There was an opaque white line along the midline of the tail and along the dorsal surface of each cephalic tentacle. There are varying numbers of scattered opaque white spots over the head, foot corners, dorsum and cerata. The foot is colorless. A color photograph appears in BEHRENS (1980a: Species No. 153) as *Coryphella* sp.



Figure 1

Dorsal view of *Sakuraoelis enosimensis* from San Francisco Bay, drawn from a color transparency. 25 mm

Buccal Armature: The radular formula of the San Francisco Bay specimens was $15-20 \times 0.1 \times 0$. BABA & HAMATANI (1965) report $18 \times 0.1 \times 0$. The teeth were broad and horse-shoe-shaped. There were 4-5 strong denticles on either side of the median cusp (Figure 3). These denticles lie in a series at nearly right angles to the axis of the central cusp. As RUDMAN (1980) states, this is quite a different arrange-

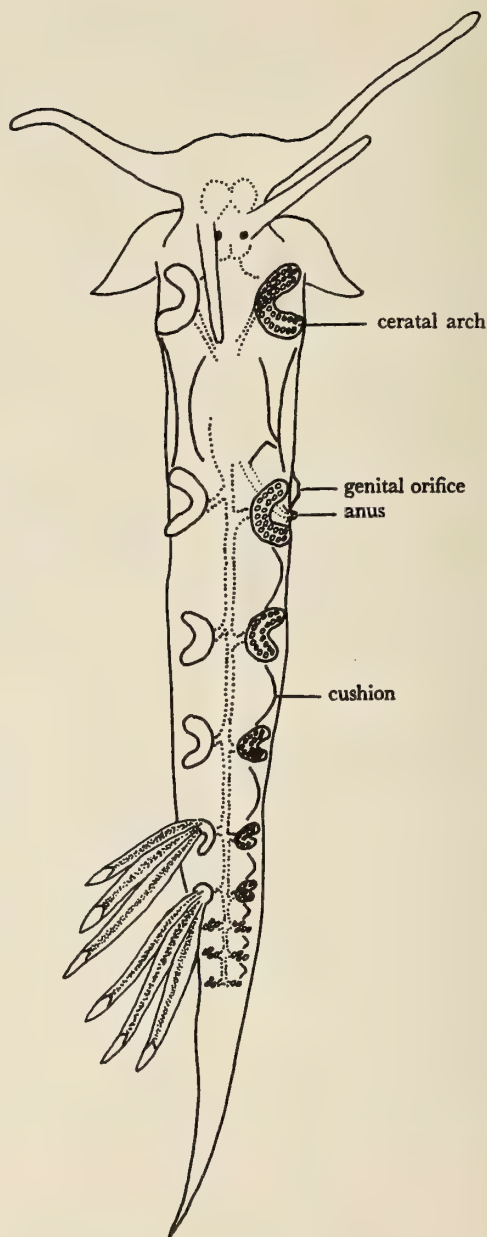


Figure 2

Diagrammatic dorsal view of *Sakuraoelis enosimensis* from San Francisco Bay, with cerata removed.

ment from the sloping flanks of most glaucids. The base of the tooth was a thick V-shaped structure only slightly wider than the blade. The jaw plates were yellow, oval

and had an indentation on the dorsal edge (Figure 4a). The masticatory border bares a double row of denticles, the longest and outermost row numbering 38-40 (Figure 4b).

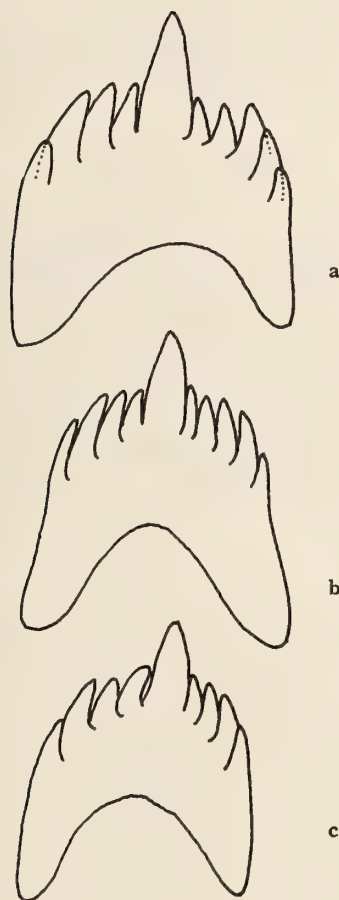


Figure 3

Radular teeth of *Sakuraeolis enosimensis* from San Francisco Bay.
a) 1st tooth, b) 8th tooth, c) 10th tooth.

Reproductive System: The penis structure is probably the most important character separating *Sakuraeolis* from the other glaucid genera (MILLER, 1974; RUDMAN, 1980). The specimens from San Francisco Bay matched the type description accurately. In the contracted state the conical-shaped penis lay in a spacious sheath. The sheath contained two fleshy folds and the characteristic accessory gland (Figure 5a). There was no stylet. In the everted state, the penis is vermiform, bending freely. The accessory gland

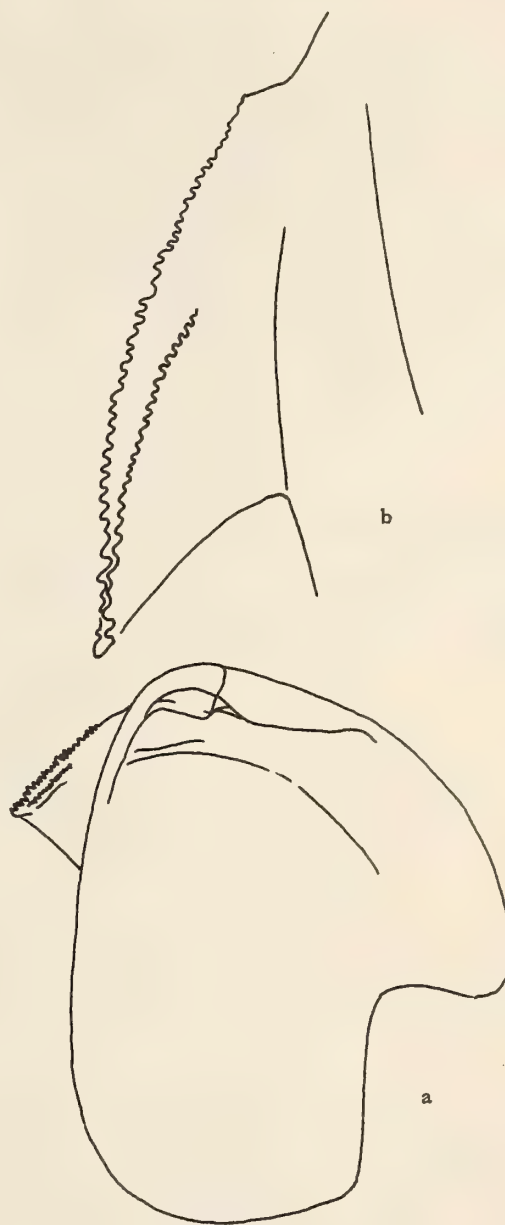


Figure 4

Jaw plate of *Sakuraeolis enosimensis* from San Francisco Bay.
a) plain view, b) masticatory edge.

protruding from the base is swollen at the distal end, which appears glandular (Figure 5b).

Ecological Observations: BABA, HAMATANI & HISAI (1956) described the egg mass of *Sakuraeolis enosimensis* (= *Hervia*

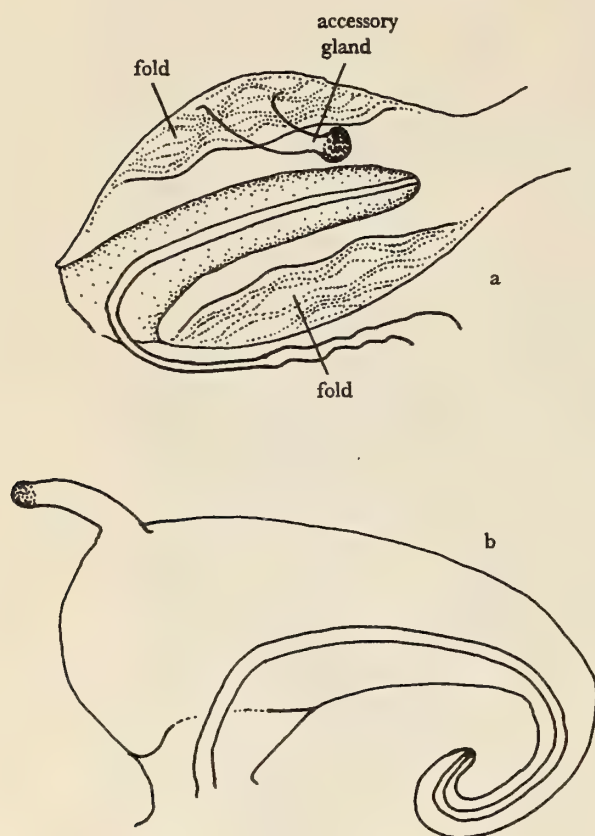


Figure 5

Distal male reproductive system of *Sakuraeolis enosimensis* from San Francisco Bay. a) contracted state, b) everted state (viewed ventrally).

ceylonica Farren). Egg masses collected with the San Francisco Bay specimens agree morphologically, except that on 2 occasions the egg string was not circular but an irregularly twisted oblong and segmented coil. RUDMAN (1980) reports the egg mass of *Sakuraeolis nungunoides* Rudman, 1980 identical to *S. enosimensis*, but different from that of *Godiva rachelae* Rudman, 1980, stating that this may give a clue to their generic relationship with other glaucids. My observations are that the egg mass may be more variable in shape. While the tightly coiled egg masses collected in San Francisco Bay closely matched those of *S. enosimensis* (see BABA *et al.* 1956: 215, fig. 6a & 6b) and *S. nungunoides* (see RUDMAN 1980: 165, fig. 17), the irregularly twisted and segmented coils more closely matched those of *G. rachelae* (see RUDMAN 1980: 160, fig. 10b & c).

Rudman (1980) derived the trivial name of *Sakuraeolis nungunoides* from the Swahili name for porcupine. He explained that this species was observed to stiffen and erect its cerata when startled or disturbed. Similar behavior was observed in *S. enosimensis*, both in the field and the laboratory when the animal was disturbed.

Voucher specimens of this species on deposit in the Department of Invertebrate Zoology, California Academy of Sciences, San Francisco, bear catalogue numbers 025782 and 025783.

DISCUSSION

MILLER (1974) included the Favorinidae in the family Glaucidae, and retained *Sakuraeolis* in the subfamily Favorininae, based on the arrangement of the cerata, being set on arches, and the morphology of the male genitalia. RUDMAN (1980) suggests that: 1) the right angle of the radular denticles to the central cusp, 2) the number of teeth in the radular ribbon, 3) the genital aperture located in the interhepatic space behind the first ceratal arch, 4) the shape of the egg mass, and 5) the extremely long cerata, might also serve as discriminants of the genus.

Within the genus, the 5 described species differ most markedly in coloration of external body parts. A tabular comparison of these features is presented in RUDMAN (1980: Table 2). On this coast *Sakuraeolis enosimensis* has gone unrecognized for years and was previously confused with *Hermisenda crassicornis* by BEHRENS & TUEL (1977). Aside from the obvious difference in rhinophores, those of *S. enosimensis* being simple, it lacks completely the characteristic blue pigmentation forming the two dorso-medial rhomboid patterns found in *H. crassicornis* (see BÜRGIN, 1965). *S. enosimensis* might also be superficially confused with a similarly colored *Coryphella* reported from Elkhorn Slough, Monterey County, California by COOPER (1980) and McDONALD & NYBAKKEN (1981). This latter species, however, has a triseriate radula, verrucose rhinophores and cerata in clusters rather than on raised arches.

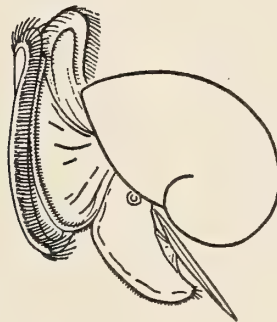
Of primary importance here is that another Japanese species has been successfully introduced into San Francisco Bay. CARLTON (1978, 1979) treats the exotic marine invertebrate introductions into the Bay. He reports 4 introduced opisthobranch species, 3 from Japanese waters. As CARLTON (1978) notes, the lack of introduced opisthobranchs prior to the early 1950's is not necessarily an indication of recent introduction to the Bay, but rather a reflection of increased interest in the opisthobranch fauna of this coast and of San Francisco Bay since then (see BEHRENS 1980b for a review of this literature).

ACKNOWLEDGMENTS

I wish to express my thanks to Joan Steinberg, Merritt Tuel, Nancy Bisetti and my two children, Jennifer and Michael Behrens, for assistance over the years collecting and documenting the presence of this species. Special thanks also to Kikutaro Baba who kindly provided me with copies of original drawings of the type specimens and of the dissections of San Francisco Bay specimens. Thanks also to James R. Lance and William B. Rudman for their critical review and comment on the manuscript.

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The Littoral and Sublittoral Polyplacophora of Diablo Cove and Vicinity, San Luis Obispo County, California

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(1 Text Figure)

INTRODUCTION

DURING THE SUMMER AND FALL of 1979 the author was afforded the opportunity to work with the mollusk collection of the Pacific Gas and Electric Department of Engineering Research Biological Laboratory at Diablo Canyon (Diablo Laboratory), San Luis Obispo County, California. The collection reflects mainly mollusks collected between the years 1968 to 1979, concentrating on Diablo Cove and vicinity, from the littoral zone to a depth of 10.7 m. It was quickly realized by the author that the area was rather unique and that the chiton fauna of the cove had not been adequately described in the literature. In addition to the lots examined in the above collection, the author was kindly allowed to collect within the littoral zone of Diablo Cove in otherwise restricted waters; sublittoral lots were provided by Lawrence "Bud" Laurent of the California Department of Fish and Game and by David Behrens of the Diablo Laboratory, to both of whom I give thanks. The collections of the California Department of Fish and Game and Lockheed, both at Diablo, were also examined. It is the purpose of this paper to present the species of littoral and sublittoral polyplacophoran mollusks encountered within this study along with their approximate littoral zonation, habitat, abundance, and sublittoral depth, and to present a listing, from the literature, of the chiton fauna reported within San Luis Obispo County.

SITE LOCALITY AND ECOLOGICAL NOTES

Diablo Cove is a well-protected indentation of the outer coast flanked to the north by Fields Cove and to the south by the Intake Cove of the Pacific Gas and Electric Nuclear Generating Station, just south of Point Buchon, at Latitude $35^{\circ}12'35''$ N, Longitude $120^{\circ}51'25''$ W (see Figure 1). The cove and vicinity offer a particularly unique opportunity for the study of littoral and sublittoral flora and fauna due to the virtually untouched nature of the

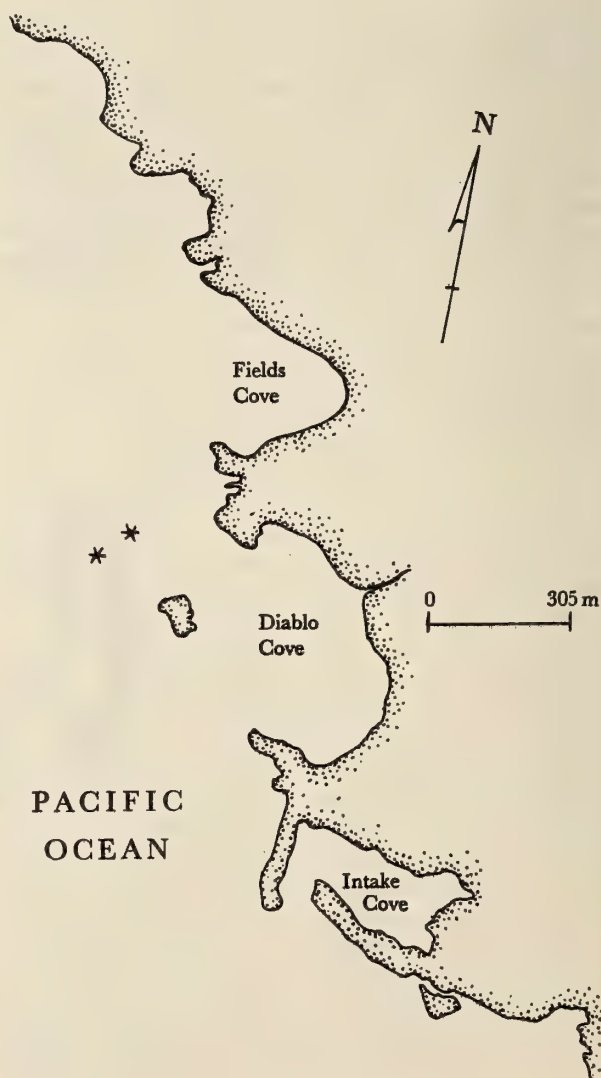


Figure 1

Diablo Cove and Vicinity, San Luis Obispo County, California

environment. The direct force of the Pacific is minimized due to the position of the area to the south of Point Buchon and to the protective nature of the surrounding rock forms.

A particularly good chiton habitat, the littoral area of Diablo Cove is abundant with manageable boulders set in a rock rubble bottom. The sublittoral environment is highly irregular with few extensive areas of sediment cover (NORTH, 1966), again an ideal situation for chitons. The areas of sediment cover appear to be composed mainly of rock or shell rubble upon which have been found chitons in great abundance.

Diablo Cove was the only area in which the author collected; the data given for Fields Cove and the Intake Cove are solely from the reference collections examined.

TERMINOLOGY

The terminology used for zonation, habitat, and abundance is the same as that proposed in PUTMAN (1981 a, b).

SYSTEMATIC ACCOUNT

Diablo Cove

Basiliochiton heathii (Pilsbry, 1898). Zone 4, under rock; common.

Callistochiton palmulatus Dall, 1878. Zone 4, under rock; uncommon.

Chaetopleura gemma Pilsbry, 1892. Zone 4, under rock; uncommon.

Cyanoplax dentiensi dentiensi (Gould, 1846).^{1 2 3 5}

Cyanoplax hartwegii (Carpenter, 1855).^{1 3 4 5}

Dendrochiton thamnopus Berry, 1911.^{1 3 4 5} At 5.8m, on stable rocky shelf; uncommon. Found in association with encrusting corallines.

Ischnochiton interstinctus (Gould, 1846). Zone 4, under rock; common. At 7.6m, on rock rubble; common to very common.

Ischnochiton regularis (Carpenter, 1855). Zone 4, under rock; uncommon.

Katharina tunicata (Wood, 1815). At 1.5 to 10.7m.^{1 3 5}

Lepidochitona keepiana (Berry, 1948).^{1 3 4 5}

Lepidopleurus rugatus (Pilsbry, 1892). Zone 4, under rock; common.

Lepidozона cooperi (Dall, 1878). Zone 4, under rock; common. At 7.6m on rock rubble; common.

Lepidozона mertensii (Middendorff, 1847). Zone 4, under rock; common. At 7.6m on rock rubble; common. At 1.5 to 10.7m.^{1 3 5}

Lepidozона sinudentata (Pilsbry, 1892). At 7.6m on rock rubble; uncommon.

Mopalia ciliata (Sowerby, 1840).^{1 2 3 4}

Mopalia hindsii hindsii (Reeve, 1847).^{1 2 3 5}

Mopalia lignosa (Gould, 1846). Zone 4, under rock; uncommon.

Mopalia lowei Pilsbry, 1918.^{1 3 4 5}

Mopalia muscosa (Gould, 1847).^{1 2 3 5}

Nuttallina californica (Reeve, 1847).^{1 3 4 5}

Placiphorella velata Dall, 1878.^{1 3 4 5}

Stenoplax fallax (Pilsbry, 1892).^{1 2 3 5}

Stenoplax heathiana Berry, 1946. Zone 4, under rock; common.

Tonicella lineata (Wood, 1815). Zone 4, under rock; common. At 1.5 to 10.7m.^{3 5}

Fields Cove

Cryptochiton stelleri (Middendorff, 1847). Juvenile, 15mm (length).^{1 2 3 5}

Cyanoplax dentiensi dentiensi (Gould, 1846).^{1 3 4 5}

Cyanoplax hartwegii (Carpenter, 1855).^{1 3 4 5}

Lepidozона mertensii (Middendorff, 1847).^{1 3 4 5}

Stenoplax heathiana Berry, 1946.^{1 3 4 5}

Intake Cove

Cyanoplax dentiensi dentiensi (Gould, 1846).^{1 2 3 5}

Mopalia ciliata (Sowerby, 1840).^{1 2 3 5}

Mopalia hindsii hindsii (Reeve, 1847).^{1 2 3 5}

Mopalia lignosa (Gould, 1846).^{1 2 3 5}

Mopalia muscosa (Gould, 1847).^{1 2 3 5}

Tonicella lineata (Wood, 1815).^{1 2 3 5}

DISCUSSION

Earlier faunal listings, although not as extensive as these, confirm or supplement the findings herein presented. In one of the first faunal listings of Diablo Cove (NORTH, 1966), *Mopalia muscosa* (Gould, 1847) was noted to exist within the littoral zone with sublittoral species listed being *Cryptochiton stelleri* (Middendorff, 1847) at 6.1 to 12.2m (the original citations being in feet), *Ischnochiton mertensii* (Middendorff, 1847) (now *Lepidozона mertensii* (Middendorff, 1847)) at 6.1m, and *Ischnochiton radians* Pilsbry, 1892 (now *Ischnochiton interstinctus* (Gould, 1846)) at 6.1m, with no other chitons noted. NORTH, ANDERSON, & CHAPMAN (1974) add a second *Tonicella* species to the intertidal list-

¹ Occurrence data based solely on museum specimens; not confirmed in habitat by the author.

² Depth information not noted with museum specimens.

³ Habitat information not noted with museum specimens.

⁴ Depth information other than "intertidal" not recorded with museum specimens.

⁵ Abundance information not recorded with museum specimens.

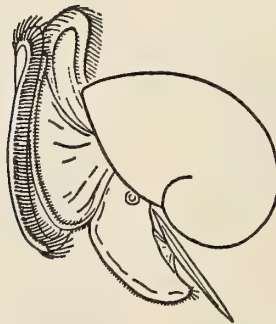
ing of Diablo Cove, *T. marmorea* (Fabricius, 1780). This addition is based on a single specimen found intertidally. The species is not known by the author to occur south of Washington state, nor has it been noted, to the author's knowledge, from the area of Diablo Cove since the publishing of the above report. For the preceding reasons and the fact that the specimen is absent from the collection at the Diablo Laboratory, the validity of the reference must be placed in doubt. Further listings in this study do, however, appear to be quite valid. These include, all from the intertidal zone, *Cyanoplax hartwegii* (Carpenter, 1855), *Katharina tunicata* (Wood, 1815), *Lepidochitona keepiana* (Berry, 1948), *Lepidozona cooperi* (Dall, 1878), *L. mertensii* (Middendorff, 1847), *L. sinudentatus* [sic] (Pilsbry, 1892), *Mopalia lowei* Pilsbry, 1918, *M. lignosa* (Gould, 1846), *Nuttallina californica* (Reeve, 1847), *Stenoplax heathiana* Berry, 1946, and *Tonicella lineata* (Wood, 1815). Most of the initial chiton laboratory identifications were made by Dr. James H. McLean of the Los Angeles Museum of Natural History, and all have been verified by the author.

Of the 47 species of polyplacophoran mollusks noted from the literature to possibly occur within the waters of San Luis Obispo County (PUTMAN, 1980, 1981 a, b), 25 can be directly attested to by the author to occur in the vicinity of Diablo Cove. A listing of the species not verified but of noted occurrence within the county, hence within the vicinity of Diablo Cove, would include (PUTMAN, 1980): *Acanthochitona avicula* (Carpenter, 1864) *Basiliochiton flectens* (Carpenter, 1863) *Callistoichiton crassicostatus* Pilsbry, 1892

Chaetopleura beanii (Carpenter, 1864)
Dendrochiton gothicus (Carpenter, 1863)
Deshayesiella (Oldroydia) percrassa (Dall, 1894)
Ischnochiton albus (Linnaeus, 1767)
*Lepidopleurus nexu*s (Carpenter, 1864)
Lepidopleurus oldroydi Dall, 1919
Lepidozona pectinulata (Pilsbry, 1892)
Lepidozona retiporosa (Carpenter, 1864)
Lepidozona scabricostata (Carpenter, 1864)
Lepidozona serrata (Carpenter, 1864)
Lepidozona willetti (Berry, 1917)
Mopalia acuta (Carpenter, 1855)
Mopalia imporcata Carpenter, 1864
Mopalia porifera Pilsbry, 1892
Placiphorella stimpsoni (Gould, 1859)
Tonicella saccharina Dall, 1878

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Predicting *Pomacea dolioides* (Reeve)

(Prosobranchia : Ampullariidae)

Weights from Linear Measurements of Their Shells

BY

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INTRODUCTION

THE AMPHIBIOUS PROSOBRANCH, *Pomacea dolioides*, is common in freshwater marshes of coastal northeastern South America (PAIN, 1950; GEIJSKES & PAIN, 1957). It is the primary food of the snail kite (*Rostrhamus sociabilis*) in Guyana, South America (SNYDER & SNYDER, 1969). While working on the feeding ecology of the snail kite in Guyana (BOURNE, 1982), it was necessary to handle large numbers of live *P. dolioides* and their discarded shells. Empty *P. dolioides* shells can be collected from under kite perches and if necessary their body weights can be estimated from linear dimensions, e.g., in order to determine energy budgets for snail kites. Before body weight estimation is possible from discarded shells the relationship between weight and linear measurements of live snails from the same population as the discarded shells must be established. Several investigators, including MENGE (1971), CAMERON & CARTER (1979), GUEDES *et al.*, (1981) and McLACHLAN & LOMBARD (1981) have predicted body weights of gastropods from linear measurements. We report the results of the relationships of linear dimensions to body weights for 1531 *P. dolioides* collected at 5 locations within coastal Guyana, from 5 habitat or patch types during 1980.

MATERIALS AND METHODS

Study Sites and Patch Types: We collected *Pomacea dolioides* in the Botanical Gardens (6°50'N; 58°09'W) and the Guyana National Park (6°50'N; 58°10'W), Turkeyen (6°50'N; 58°08'W), Vryheid's Lust (6°50'N; 58°06'W), and Burma (6°28'N; 57°45'W), Guyana. All of these locations are on the eroded coastal flood plain bounded by the Abary River on the East and the Demerara River on the west. Several other rivers and drainage canals dissect the landscape and discharge their waters into the Atlantic Ocean to the north. Descriptions of the climate, geology,

flora and fauna of Guyana's coast are available in HARRISON *et al.* (1913), PAIN (1950), GIGLIOLI (1959), CUMMINGS (1965), SNYDER (1966), and POONAI (1970).

Five snail habitat or patch types were defined as follows: (1) shallow drainage ditches <0.5m deep and <1m wide (little ditch); (2) shallow drainage ditches <1m wide (big ditch); (3) ponds of varying areal coverage, but <1m deep (pond); (4) natural sedge and grass wetlands with water depths varying from 80mm to 0.5m (meadow); and (5) flooded ricefields with varying water depths of 105 to 250mm (ricefield).

Sampling and Measuring: Snails were sampled from June to November 1980. We used modifications of WIENS' (1969) line transect method to obtain restricted random samples. Only visible *Pomacea dolioides* at or near the surface of turbid water were gathered by hand at each sample point. Spat sized individuals (<10mm wide or <0.25g whole fresh weight) were ignored. This was done to simulate the visual hunting behavior of the snail kite. About 100 snails were taken from each patch type present at each location.

The snails were dried and cleaned of adhering matter with laboratory paper towels. Height (the distance between the shell apex and the lower margin of the peristome) and width (the maximum shell diameter) were measured to the nearest 1mm by dividers and metric ruler. Weights were recorded for each snail on a 30g or 100g spring scale to the nearest 0.25g. A total of 1479 *Pomacea dolioides* were processed.

Fifty-two snails were collected on 5 November from a big ditch in the Guyana National Park. Individuals visually judged to be smaller than the mean size taken by snail kites were ignored. Shell measurements and whole fresh weights were recorded. The soft tissue was excised by severing the columellar muscle with a sharply decurved piece of wire and the operculum was removed. Individuals were sexed by inspection of gonads. The tissue mass was blotted dry in filter paper and fresh weights recorded to the nearest 0.01g. Dry weights to the nearest 0.01g were

obtained after oven drying at 60°C for 48 hours. We dropped 7 snails from this sample because it was impossible to get all of the soft tissues out of their shells. Therefore, statistical analyses were performed on 45 snails.

Statistical Methods: We used conventional least squares regression methods to explore relationships among the various parameters. Regression was used to test for the significance of the linear relationships between the pertinent variables and to develop equations which might be useful for predictive purposes. Analysis of covariance was used to compare regression equations from different populations. Residual analysis was performed in all cases to test the assumptions of the regression and analysis of covariance models.

The relationship between length and weight of some organisms is commonly expressed as a logarithmic function (e.g., RICKER, 1975). The equation relating length to weight takes the form: $\text{weight} = e^a \text{length}^\beta$, where a and β are the parameters of the model for a given population of organisms. This equation may be expressed in linear form as follows: $\log_e \text{weight} = a + \beta \log_e (\text{length})$. This will be referred to as a log-log regression.

Expressions were developed separately for each patch type within each location, yielding a total of 14 individual regressions. These regressions were then compared across patch types (within location) using the analysis of covariance (NETER & WASSERMAN, 1974).

A sample of 45 snails was obtained from the pond patch type within the Guyana National Park. Data from this sample were used to develop predictive equations for the

dry weight of an individual based on whole fresh weight or width. Equations were developed for the entire sample and separately for males and females. The equations for males and females were compared using analysis of covariance.

RESULTS

The α and β parameters along with R^2 values for the regressions are summarized by location and patch type (Table 1). Analysis of residuals showed no significant departures from the assumptions of the regression model. The lowest R^2 value for any regression equation was 0.88 (Burma, big ditch) (Table 1), and all regressions were significant below the 0.0001 level. Thus, the log (length)-log (weight) model commonly applied to problems of scaling in the evolution of animal size and to fisheries allometry (e.g., Gould, 1966, 1971; RICKER, 1971, 1975) appears to hold quite well for *Pomacea dolioides*, and this relationship may be used to predict whole weight from width with a high degree of confidence. Tolerance intervals indicate that actual predictive precision is best at or near the mean.

Analysis of covariance indicated that for 3 locations (Botanical Gardens, Guyana National Park, and Vryheid's Lust) the regressions were clearly different across patches. For the remaining 2 locations (Burma and Turkeyen), the hypothesis of equal regressions could be accepted marginally. However, combining regressions meant a reduction in R^2 values and an increased standard error (SE)

Table 1

Log-log regressions of width on weight for coastal Guyana *Pomacea dolioides*, June-November 1980.

Location	Patch	N	α	β	R^2 *	SE***
Burma	Big Ditch	102	-7.51	2.73	0.88	2.64
	Little Ditch**	77	-7.91	2.85	0.90	2.13
	Meadow	103	-8.09	2.89	0.93	3.37
	Ricefield	103	-7.94	2.84	0.92	3.56
Botanical Gardens	Big Ditch	116	-8.59	3.01	0.95	2.77
	Little Ditch	117	-8.30	2.92	0.93	2.29
	Meadow	112	-8.32	2.92	0.97	1.99
	Pond	110	-8.15	2.90	0.95	3.01
Guyana National Park	Big Ditch	122	-8.62	3.00	0.94	2.87
	Pond	103	-7.87	2.83	0.93	3.38
Turkeyen	Big Ditch	103	-8.26	2.91	0.93	2.99
	Meadow	104	-8.18	2.90	0.93	3.20
Vryheid's Lust	Big Ditch	106	-7.58	2.72	0.98	1.20
	Meadow	101	-6.70	2.50	0.90	3.51

* $P < 0.0001$ in all cases.

**Really the Rice Research Station at Burma.

*** R^2 and SE expressed in terms of the raw data by antitransforming predicted values.

Table 2

Log-log regressions of whole weight on dry weight and width on dry weight for 18 male and 27 female *Pomacea dolioides* collected at Guyana National Park, Georgetown, 5 November 1980 from a big ditch.

Sex	Variables	α	β	R ² **	SE***
Male	WW on DW*	-2.73	1.02	0.75	0.18
Female	WW on DW	-2.27	0.91	0.62	0.18
Male	W on DW	-9.36	2.49	0.56	0.24
Female	W on DW	-8.31	2.26	0.50	0.20
Both	WW on DW	-2.75	1.04	0.76	0.18
Both	W on DW	-10.09	2.70	0.63	0.22

*WW = whole weight, DW = dry weight, W = width.

**P < 0.0001 in all cases.

***R² and SE expressed in terms of the raw data by antitransforming predicted values.

in some cases. For predictive precision, then, it was decided to let the separate regressions stand.

Regressions were also developed within the sexes to relate dry weight to whole fresh weight or width. As far as predictive ability and meeting assumptions are concerned \log_e (dry weight) versus whole fresh weight, and \log_e (dry weight) versus \log_e (whole fresh weight) performed equally well (Table 2). However, the analysis of covariance indicated that only the \log_e (dry weight) - \log_e (whole weight) regressions could be combined across sex, making this the more useful relationship (Table 2). When the regression is developed ignoring sex, the equation is: dry weight = $e^{-2.75}$ (whole fresh weight)^{1.04}. This regression was significant (Table 2).

The regression derived to relate dry weight to width also took a log-log form (Table 2). The equation was dry weight = $e^{-10.09}$ (width)^{2.70}. However, the analysis of covariance indicated that the intercepts for the regressions by sex were not equal. This means an overall equation, although possibly still useable, would show a consistent bias in prediction depending on the sex of the individual.

DISCUSSION

At 3 locations (the Botanical Gardens, Guyana National Park, and Vryheid's Lust) cross patch comparisons of the width-weight relationships indicated significant differences, while comparisons at Burma and Turkeyen showed no significant differences in relationships. Apparently there are 4 major reasons for these patch to patch differences. The reasons discussed below may or may not be mutually exclusive.

Firstly, some patches completely dry up in the late dry season (September to November 1980), e.g., the big ditch and meadow at Vryheid's Lust, little ditch and meadow in the Botanical Gardens, and some meadows and ricefields at Burma. In the absence of standing water *Pomacea dolioides* aestivates. This affects growth patterns (BURKY, 1974) and probably influences changes in surface area to volume relationships (GOULD, 1971). Secondly, although snail food availability was not measured, the big ditches and ponds in the Botanical Gardens and Guyana National

Park appeared to provide abundant year-round supplies of aquatic algae and *Nymphaea* spp. lilies, whereas the other patches in other locations appeared to provide food in flushes, influenced by water availability. Thirdly, as this study indicates, there are sexual weight differences. It has also been shown that females with maturing eggs weigh more than the mean for their shell dimensions (GUEDES *et al.*, 1981). If a sample from a particular patch is biased towards females with maturing eggs, significant differences across patches could be expected. This coupled with the fact that reproductive regimes vary from patch to patch because of water availability problems. Thus, we would expect varying stages of egg maturation to account for some of the significant differences in width-weight relationships across patches. Finally, we cannot rule out effects due to differences in collection dates. This could produce differences in the measurement-weight relationships through an aging effect. Similar intraspecific size related differences due to age have been reported for fishes (RICKER, 1971, 1975), and gastropods (GELDIAY, 1956).

SUMMARY

In Guyana, South America, the amphibious prosobranch, *Pomacea dolioides* (Reeve), is very common in coastal freshwater marshes, ricefields, drainage and irrigation ditches, and ponds. From June to November 1980, 1531 *P. dolioides* were collected and weighed and their shells were measured to elucidate the relationships between linear measurements, whole fresh weights and excised dry weights.

The snails were collected at the Botanical Gardens, Guyana National Park, Turkeyen, Vryheid's Lust and Burma from 5 patch types, i.e., little ditches, big ditches, ponds, meadows, and ricefields. Least squares regressions indicated the significance of the linear relationships of the measured variables and allowed us to develop a predictive equation of the form \log_e (weight) = $\alpha + \beta \log_e$ (width), where α and β are coefficients of the equation derived from the regressions.

Whole fresh weights were predicted from width measurements of shells, but there were location and patch differences. Therefore, separate regressions were used for each

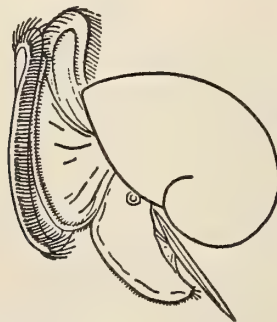
location and patch to improve predictive precision. Sexual differences were also found for 45 snails that were sacrificed, sexed, and their flesh dried. However, \log_e (dry weight) against \log_e (whole fresh weight) regressions could be combined across the sexes. This relationship is more useful for studies where destructive sampling is not desirable or is impossible.

ACKNOWLEDGMENTS

We thank Sheila Bornyas, Joyce Fredericks, Susan Milan, Patricia Voice, and Drs. Bernard and Gregory Bourne for assisting in the field. Dr. James Diana kindly provided laboratory facilities. Christopher Hoogendyk, Drs. Gary Belovsky, Gary Fowler, Bobbi Low, Robert Storer, and Alex Tompa provided critical reviews of an early draft of this paper. This work was supported in part by a Rackham Minority Fellowship, a Rackham Dissertation Grant, the School of Natural Resources of The University of Michigan, the Chapman Memorial Fund, Sigma Xi, and Jane E. Stevens. Data are taken from Bourne's dissertation submitted to The University of Michigan.

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Escape Response of an Infaunal Clam
Ensis directus Conrad 1843,
to a Predatory Snail, *Polinices duplicatus* Say 1822.

BY

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INTRODUCTION

BEHAVIOR THAT INCREASES the risk of predation is usually attributed to infection by a parasite, which thereby increases its chances of moving to the next host. CURIO (1976) reviews several cases of increased prey visibility, including a peculiar crawling behavior by an infaunal marine bivalve, *Macoma balthica* Linnaeus, 1758, infected by trematodes (SWENNEN, 1969). In this note I report a behavior that increased the visibility of an infaunal bivalve to gull predators, but which was not due to infection by a parasite. I show that this behavior is an avoidance response to a tactile predator, the moon snail, *Polinices duplicatus* Say, 1822. The palaeontological implications of this interaction were pointed out to me by J. Levinton.

LOCATION & STUDY SITE

The study was carried out on the intertidal flats at Plymouth, a coastal lagoon 80 km south of Boston, Massachusetts. Observations were made from 1975 through 1979. Experimental studies were carried out on White Flat (41°79'N, 70°40'W) during 1979. This flat grades from silty sand on its western (shoreward) side to fine well-sorted sand on its eastern side. An area of one kilometer by one-half kilometer is exposed twice a day for two to three hours. Razor clams ranging in size from 1 to 15 cm in length were found on this flat in five successive years. Two naticids inhabited this flat: *Polinices duplicatus* and *P. heros* Say, 1822. The preferred prey of *P. duplicatus* has been described by EDWARDS (1975), while WILTSE (1978) has described the impact of this predator on prey numbers at a nearby lagoon, Barnstable.

RESULTS

The experiments grew out of a series of observations made throughout the lagoon over a 5 year period. Razor clams (*Ensis directus*) are active burrowers that normally dig rapidly into the sand when disturbed. Despite this, some clams were observed flipping themselves vigorously over the surface of the sand at low tide. This increased their risk of predation by gulls (*Larus delawarensis* Ord, 1815). Gulls were frequently observed feeding on razor clams, but never observed pulling a clam from the sand, or pecking at the sand to find prey. Clams dig rapidly into the sand after short excursions. The brief exposure was not consistent with the hypothesis of behavior modified by a parasite. Two clams found flipping over the flats were dissected. Both were free of trematodes.

The behavior occurred at night, when clams could be located by the squirting sounds made as the clams flipped over the sand. Thus the behavior was not a response to deteriorating environmental conditions caused by heating of the sand during daytime low tides.

A chance observation suggested an alternative hypothesis. Some razor clams were observed with the siphon end protruding well out of the sand. In every case the foot of the clam, beneath the surface of the sand, was held by a predator; either a naticid snail (*Polinices duplicatus*) or a nemertean (*Cerebratulus lacteus* Leidy, 1851). This observation suggested that razor clams leave the sand to escape attack by these relatively slow moving predators.

To test the response of razor clams to naticids I pushed a clam part way into the sand directly in the path of a crawling naticid. As soon as the leading edge of the snail's foot touched the clam it dug rapidly into the sand. The snail dug rapidly down the hole left by the clam. After

a minute or two the clam emerged foot first from the sand, within a meter or two of the point where it started. The slightly curved shell of the clam evidently contributed to the re-emergence. Upon emergence the clam twisted its foot back toward the siphon end, pushing down onto the sand with the foot until the shell rose enough out of the sand to topple over. The clam then propelled itself over the sand by a series of vigorous lashes with the foot, combined with rapid ejections of water along the ventral side of the foot.

I repeated the experiment with 10 clams collected nearby. In 5 cases the clams emerged from the sand at a distance from the point of attack, and flipped away. Clams that emerged in areas without standing water traveled less than a half meter before digging into the sand. Clams that emerged in puddles of standing water would propel themselves several meters through the water before digging back into the sand. In 3 cases the clam never re-appeared, and the snail soon re-appeared without the clam. In the remaining cases the clam emerged from the sand siphon first. Digging away the sand revealed the naticid grasping the clam and working its way downward toward the foot of the clam. The snail attacked the foot, leaving no hole in the clam shell to mark its attack.

I repeated the experiments with two common molluscs that co-occur with naticids on White flat. The gastropod *Nassarius trivittatus* Say, 1822 responded by rapid crawling or by flipping across the sand by vigorous contortions of the foot. *Tellina agilis* (Stimpson, 1857) did not always respond—some individuals flipped themselves by vigorous twists of the foot.

The experiment was repeated by collecting two species of snails from a nearby muddy flat, which was not inhabited by naticids. In each trial I placed a new snail in the path of an oncoming naticid, as in previous experiments. I repeated the experiment with five periwinkles (*Littorina littorea* (Linnaeus, 1758) and five mud snails (*Ilyanassa* [*Nassarius*] *obsoleta* Say, 1822) using 10 different naticids. None of the snails showed an escape response in response to touch by the naticid. The naticids did not complete their attack and eventually crawled away.

DISCUSSION

Escape responses result from direct contact with a predator, while avoidance responses are made at a distance, often

through chemical cues (PHILLIPS, 1977). Escape responses have been reported most frequently in gastropods (GORE, 1966; KOHN, 1961), but have also been found in scallops and an anemone (YENTSCH & PIERCE, 1955). Generalizations about the occurrence of escape responses have not been forthcoming, although MACKIE (1972) suggested that saponins were responsible for escape responses to asteroids. The reported cases of escape response by molluscs have all been to tactile predators (asteroids, gastropods), rather than visual predators (birds, crabs, etc). Escape responses vary in their occurrence among species within a habitat, and their specificity relative to any given predator (MACKIE, *op. cit.*). At Plymouth, escape responses were not found in two common gastropods that do not occupy the same habitat as naticids. This degree of specificity suggests that escape responses are a co-evolved interaction between a predator and its prey. It would be interesting to examine the role of inheritance and learning in the maintenance of escape responses.

The fact that naticids grasped the clam beneath the substrate, with the siphon pointing upward, has some implications for interpreting the fossil record. Naticids left no trace of their attack on razor clams because they attacked the foot rather than drilling through the shell. A bed of razor clams would remain in life position after attack by naticids, and would appear to have been killed by burial.

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Retention of Label of Leucine-U-¹⁴C in the Haemolymph of *Pila globosa* (Swainson) as a Function of Sex and Long-term Aestivation

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AND

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INTRODUCTION

IN THE INDIAN APPLE snail *Pila* the biochemistry and physiology of short-term aestivation have been worked out considerably (MEENAKSHI, 1956a, 1956b, 1957, 1964; REDDY, 1965, 1967; REDDY & RAMAMURTHI, 1973). Examination of the above-mentioned aspects with reference to long-term aestivation has just commenced (CHANDRASEKHARAM *et al.*, 1979).

In this communication the rate of retention of label of injected leucine-U-¹⁴C in the haemolymph of *Pila globosa* is presented as a function of sex and long-term (25 months) aestivation.

MATERIAL AND METHODS

The method of preparation of snails for aestivation was according to KRISHNAMOORTHY (1968). The procedure with regard to injection of radio-isotope into active (= normal) and aestivated snails was described by REDDY & RAMAMURTHI (1973). Details regarding collection of haemolymph and radiometry of the same were given by CHANDRASEKHARAM *et al.* (1979).

RESULTS AND DISCUSSION

The data on 'volume-specific recovery' (VSR) of label of injected leucine-U-¹⁴C in the haemolymph of *Pila globosa* show clear sex-based differences (Table 1). The VSR of 'male' snails is considerably higher than in 'female' snails

Volume-specific recovery of label (VSR)
in the haemolymph of *Pila globosa*
injected with leucine-U-¹⁴C as a function of sex
and long-term (25 month) aestivation.¹

Condition Sex	Active (= normal) A	Aestivated E	A:E ratio
Female	245 ²	1814	100 : 740
Male	434	1055	100 : 241
F:M ratio	100 : 177	100 : 58	

¹Values are expressed as dpm. ml haemolymph⁻¹

²Values are averages of triplicate planchettings; Number of snails used for injection of isotope: ♂ A:3; ♀ A:2; E:4; Radiometry carried out on haemolymph collected from the snails 18 h post-injection (of isotope); Known volume of whole (untreated) haemolymph planchettied on stainless steel planchette and dried was used for radiometry in an end-window gas-flow proportional counter (ECIL, Hyderabad); correction made for self-absorption.

in normal (active) condition. The long-term-aestivated snails (of both sexes) show increased VSRs of label in haemolymph. These observations may suggest that in the aestivated snails, the injected isotope is not 'dissipated' from haemolymph as fast as it is in the active snails. The decrement of cardiac rhythmicity and concomitant impairment of circulatory capability CHANDRASEKHARAM *et al.* (1979) seems to explain this lessened 'isotope-dissipation' from haemolymph in aestivated snails only partially. If impairment of circulatory capability alone were to cause increased retention of label, there should have been greater retention in male *Pila* with a 65.6% reduction in cardiac rhythmicity (after 25-month aestivation-sojourn) than in the female with a 56.6% reduction of cardiac rhythmicity (CHANDRASEKHARAM *et al.*, 1979). The female snail on the

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contrary shows a considerably higher retention of label: in the female increase in VSR or retention of label is 640% in 'aestivated haemolymph' over 'normal haemolymph,' whereas in the male the increase is only 141%. It should be clear from the above consideration that, besides reduction of circulatory capability, alterations of rates of haemolymph tissue transactions (permeation) of substance are involved in producing the above-mentioned 'label retention picture' highlighting male-female contrast. Earlier (CHANDRASEKHARAM *et al.*, 1979) it has been shown that in the female, label retention from injected palmitate- $U-^{14}C$ in aestivated haemolymph shows an increase of 1303% over normal, the increase of label retention for glucose- $U-^{14}C$ is 511%. These reports provide further probation for the concept of differential alterations of rates of permeation of substances in haemolymph-tissue transactions during aestivation in the snail.

SUMMARY

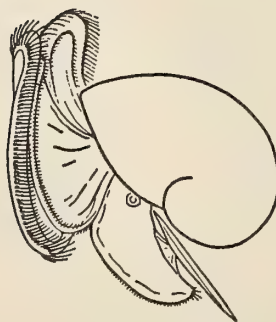
The normal (= active) female *Pila globosa* shows considerably lower retention of label in haemolymph (= volume-specific recovery of label, VSR) from injected leucine- $U-^{14}C$ than the male. After long-term (25 months) aestivation in female VSR increases by 640% in aestivated snails over normal snails; for the male the increase in VSR is only 141%.

ACKNOWLEDGMENTS

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An Underwater Measure of *Octopus* Size

BY

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(1 Text Figure)

VITAL TO ANY FIELD STUDY of animal ecology and behavior is a measure of size which can be made quickly and reliably, and which causes minimum disturbance to the subjects. Studies of *Octopus* demography, physiology and growth have relied on determinations of body weight (WELLS, 1960; NIXON, 1966; WELLS & WELLS, 1970; VAN HEUKELEM, 1973; MANGOLD & FROESCH, 1977; HARTWICK *et al.*, 1978; WODINSKY, 1978), length measures (ITAMI *et al.*, 1963; WOLTERDING, 1971; HATANAKA, 1979; GUERRA, 1981) or both (NIXON, 1969; MANGOLD & BOLETZKY, 1973; HANLON, 1975; OPRESKO & THOMAS, 1975). The purpose of this paper is to report the utility of mantle length as a field measure of the size of *Octopus briareus* Robson, 1929. While body weight determinations necessitate the trauma of bringing the animals to the surface (see below), mantle length may be measured without removing the *Octopus* from their habitat.

During June and July, 1980, 55 specimens of *Octopus briareus* were collected alive by SCUBA diving from shore in Sweetings Pond, a salt water lake on Eleuthera Island,

Bahamas, centered at approximately 25°21'35" N latitude, 76°30'40" W longitude. *Octopus briareus* occur there commonly within a depth range of approximately -2 to -7.5 m. Four or five *Octopus* were captured per dive and placed in individual plastic containers or glass jars. They were brought ashore as quickly as possible, where they were measured, sexed and weighed. Survivors of the procedure were then released well away from the collecting area.

Two easily obtained measurements were taken under water, in the shallows of the lake, with a plastic-coated, metric measuring tape¹:

1. mantle length—the distance from the mantle apex to the point midway between the eyes, and
2. head width—the greatest width of the head across the eyes.

¹ Calipers were not employed because they are extremely difficult to use on struggling, respiring *Octopus*. Furthermore, the animals may be injured as a result.

Table 1

Correlations of body weight (g) with mantle length and head width (cm), after logarithmic transformation of the data. *N*, sample size; *r*, product-moment correlation coefficient; major axis slopes and y-intercepts by the method of principal axes (SOKAL & ROHLF, 1969: 526-532). Females brooding eggs were excluded from the analysis (see text).

Sex categories	<i>N</i>	<i>r</i>	Significance of <i>r</i>	slope	y-intercept	95% confidence limits of slope
Body weight (abscissa) with mantle length (ordinate)						
Males, females and juveniles	55	0.902	$p < 0.00001$	0.261	0.583	0.294, 0.228
Males and females	49	0.804	$p < 0.00001$	0.366	0.083	0.444, 0.292
Males	37	0.739	$p < 0.00001$	0.357	0.120	0.467, 0.255
Females	12	0.891	$p < 0.00005$	0.374	0.060	0.487, 0.269
Body weight (abscissa) with head width (ordinate)						
Males, females and juveniles	55	0.854	$p < 0.00001$	0.195	0.127	0.226, 0.163
Males and females	49	0.722	$p < 0.00001$	0.300	-0.375	0.383, 0.221
Males	37	0.699	$p < 0.00001$	0.344	-0.583	0.462, 0.234
Females	12	0.796	$p < 0.001$	0.267	-0.222	0.387, 0.155

ROBSON (1929: 25) refers to these as "dorsal mantle length" and "interocular distance," respectively; I have adopted the more current terminology of VOSS (1963) and BURGESS (1966). Mantle length was measured with the mantle fully inflated. Measurements were made to the nearest 0.25 cm; given the plasticity of the *Octopus* body and the fact that the measurements were made under water, greater precision was not possible.

Sex was determined by the presence of the hectocotylized third right arm in males. In almost all males, the penis was also visible, through the underside of the mantle. Six individuals, ≤ 3.0 cm in mantle length, could not be sexed in the field, and were called "juveniles," following MANGOLD-WIRZ (1963: 9). Females guarding eggs were not included because *Octopus* in this condition feed only rarely and lose weight (WOLTERDING, 1971: 67-70; WELLS, 1978: 95; WODINSKY, 1978).

Prior to weighing, each animal was placed in an empty, covered, plastic container for a few minutes. Water was then drained from the container and the *Octopus* weighed. This procedure allowed water to run off the body and also drained most of the water from the mantle cavity. The precision of the scale allowed measurements to the nearest 1g. Anaesthesia was considered, so that the mantle cavity could be drained completely (VAN HEUKELEM, 1973); however, the precision of the scale did not warrant its use. NIXON (1969) does not consider anaesthesia necessary for weighing *Octopus*².

Table 1 presents the results of correlation analysis comparing body weight with mantle length and head width (logarithmic transformations). Equations of the best fit lines were calculated by the method of principal axes (SOKAL & ROHLF, 1969, pp. 536-532; calculated on an Apple Plus computer, program by K. P. Sebens). All of the correlations in Table 1 are highly significant, but mantle length gives consistently higher product-moment correlation coefficients, r . Mantle length is, therefore, the field measure of choice. The mantle length correlations for all individuals, and for males and females taken together, are shown in Figure 1. Separate correlations for juveniles await further data collection.

In both sets of correlations (Table 1), the 95 percent confidence limits of the major axis slopes include 0.333, except when juveniles are included. A slope of 0.333 is expected for isometric growth. The lowered slopes due to the inclusion of juveniles may imply negative allometry,

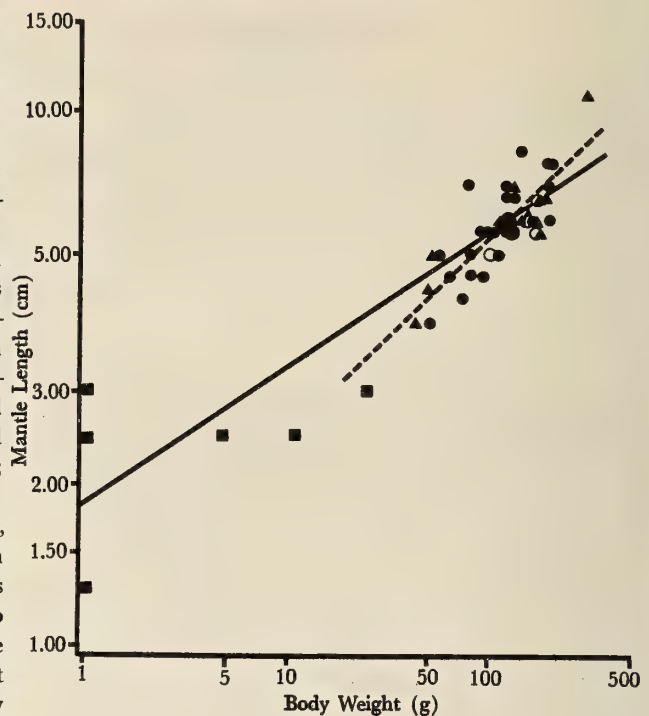


Figure 1

Correlations of body weight with mantle length of *Octopus briareus*. Data points: small, solid circle = male; open circle = two identical points for males; large, solid circle = three identical points for males; triangle = female; square = juvenile. Principal axis lines (SOKAL & ROHLF, 1969): solid line (all data), $y = 1.79x^{0.261}$; broken line (males and females only), $y = 1.09x^{0.366}$.

as HANLON (1975: 49-51) found for laboratory-reared *Octopus briareus*; it must be remembered, however, that the percent errors in the measurements are greatest for the juveniles.

Mantle length has been used as a size measure for *Octopus vulgaris* (NIXON, 1969; GUERRA, 1981) and *O. joubini* (OPRESKO & THOMAS, 1975), as well as for *O. briareus* (WOLTERDING, 1971; HANLON, 1975). NIXON (1969: fig. 1) presents the same type of correlation for *Octopus vulgaris* ($r = 0.982$, 65 degrees of freedom, $p < 0.001$) as I have shown in Figure 1 for *O. briareus*. The usefulness of mantle length as an underwater measure cannot be over-emphasized. Measurements involving arm length are impossible with unanaesthetized *Octopus*; like body weight, they require bringing the animals to the surface. Approximately 30 percent mortality occurred as a result of the combination of transport to shore and the weighing procedure in this study. Other individuals were obviously traumatized. Such effects can be devastating to field studies of ecology and behavior.

² Individuals that were missing arms or parts of arms were excluded.

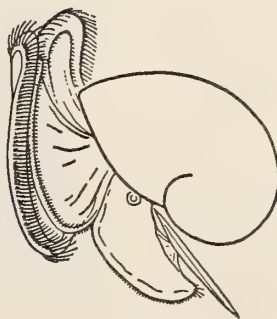
In summary, mantle length satisfies the three criteria of a good measure of *Octopus briareus* size. At an underwater study site, an individual can be captured, measured (and sexed) quickly, and then released unharmed. The highly significant relationship with body weight vouches for the reliability of the mantle length measure.

ACKNOWLEDGMENTS

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NOTES & NEWS

Bivonia sutilis (Mörch, 1862)

Re-Established as a Valid Species

BY

SANDRA M. GARDNER

Since 1862, when Otto A. Mörch described a vermetid, *Bivonia sutilis* from a single specimen growing on one valve of *Venus subimbricata* Sowerby, from western Central America, no material which matched his description has been recognized or identified until now.

The holotype of this shell is in the British Museum (Natural History), Registry No. 197878.

With the passage of over 100 years and without material clearly identifiable as *Bivonia sutilis*, the species was synonymized, with question, with *Aletes centiquadrus* (Valenciennes, 1846) by KEEN in 1958 and with *Tripsycha (Eualetes) centiquadra* (Valenciennes, 1846) by KEEN in 1971.

A photograph of the holotype of *Bivonia sutilis* shows a growth habit of early irregular, almost planorboid, coiling which changes as the animal grows, to one vertical tube which then turns downward in the manner of a hook and finally reattaches itself to the substrate.

Material collected in the Gulf of California in 1978 and 1980 by Carol Skoglund matches the picture of the type and has been identified as the species *Bivonia sutilis* by Dr. Keen, who has a photograph of the type in her possession. A single specimen collected by Andre Villanueva at Cebu, the Philippines, in 1981 shows a marked resemblance to the Gulf of California material.

Most of the modern specimens have a slightly different growth habit, with the mature vertical tube remaining free. This suggests that the reattachment of the mature tube to the substrate may be an occasional trait, not necessarily characteristic of the animal's growth. Modern specimens have smoother sculpture than that of the holotype, indicating variation in the species.

The generic assignment of this species remains in doubt. The form is a white tube of 7 to 9 mm diameter with earlier whorls coiled like those of a *Serpulorbis* (Sassi, 1827).

As the animal reaches maturity it forms a vertical tube which at some midway point breaks off and starts growing another tube at an angle. The original broken tube remains as a "scar."

Although this growth pattern resembles that of a *Serpulorbis*, generic allocation either to *Tripsycha* or to *Serpulorbis* rests on the basis of the presence or absence of an operculum; *Serpulorbis* is inoperculate. Observation of living animals in the field will be necessary for generic identification.

Mörch notes, with his description of *Bivonia sutilis*, that a similar form, *Vermetus semisurrectus* (Bivona, 1832) occurs in the Mediterranean. This information, taken with these specimens from the type locality of the Gulf of California and from the Indo-Pacific raises the possibility that this species may be distributed widely beyond western Central America. This would have to be confirmed by anatomical study of the soft parts.

ACKNOWLEDGMENT

Dr. Myra Keen kindly identified material which came into my possession and generously assisted me with the preparation of this paper, for which I am most appreciative.

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IMPORTANT NOTICE

If the address sheet of this issue is PINK, it is to indicate that your dues remittance had not arrived at the time the mailing was prepared (*i.e.*, by March 1, 1982). We wish to take this opportunity to remind our Members that a reinstatement fee of one dollar becomes due if membership renewals have not been received by C. M. S., Inc. by April 15, 1982. However, in view of the unreliability of the postal service, members should not be alarmed by this notice as their remittances may be received between the

first of March and the date of mailing this issue on April 1. From overseas addresses we must allow a minimum of 6 weeks for surface mail. On the other hand, it is possible that the envelope and dues notice enclosed between pages 292 and 293 of the January issue have escaped your attention. If so, now is the time to use them to avoid interruption in the delivery of this periodical.

A SURPRISE FROM THE POSTAL SERVICE:

On February 1 we were informed that effective on January 10, 1982 the postage rate for second class matter (the Veliger, in our case) within the United States had been increased by "about 50%." Exact figures, however, were not given us!

Unfortunately, this information not being available to us when the subscription rates for volume 25 had to be established, we were unable to make the necessary adjustment in our mailing charges. We will be forced, however, to increase our rates when volume 26 is being considered. Our by-laws, written and adopted in times before the Postal Service was instituted, forbid us to ask for additional payments now.

Subscription Rates and Membership Dues

At its regular meeting on October 27, 1981, the Executive Board of the California Malacozoological Society decided, in spite of inflationary pressures, to maintain the same dues and subscription schedules as are in effect at present. This means that membership dues (which include a subscription to the Veliger) will remain at US\$ 18.50 plus mailing charges of US\$ 1.50 for domestic addresses and US\$ 5.00 for all foreign addresses (including Canada and Mexico). The initiation fee for new members remains at US\$ 2.00; reinstatement fee, due if membership renewals are not made to reach the Society on or before April 15 preceding the start of the new volume, will also remain at the old level of US\$ 1.00. Further, the need for a new application for membership and the payment of a new

initiation fee, if membership has been permitted to lapse through non-payment of dues for 11 months after the original deadline was reaffirmed. Similarly, the need to require the inclusion of a self-addressed, stamped envelope, if a receipt is required, was re-affirmed.

In view of the deplorable fact that the postal services throughout the world seem to become ever more expensive and also more unreliable, members are urged to lodge complaints for intolerable delays in deliveries of their journals with their local postmasters. Most likely, this will not result in better service, at least not immediately, but it may be hoped that in the long run it will lead to some improvement. Complaints to the Society cannot lead to any improvement, since we already do more than the requirements of the postal service in respect to second class mailings stipulate.

W. S. M.

The University of Redlands, Redlands, California, will be the site of the 15th Annual Meeting of the Western Society of Malacologists, June 20-23, 1982.

Symposia on the Bivalvia and the Muricidae are being planned as well as a work shop on shell photography.

New meeting facilities are being made available that should add to the comfort of those attending the scientific sessions and the displays.

For more information, please contact:

Ms. Kit Stewart
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The NINE DIGIT ZIP code

is coming! And although the Postmaster General keeps asserting that its use is entirely voluntary, there are certain consequences to be anticipated if it is not used. One consequence which will affect us directly is the fact that "addressed pieces with the 9 digit code" will be entitled to a discount (this applies to bulk mailings, such as the quarterly dispatch of our journal). In other words, if the code is not used, we have to pay what really amounts to a penalty. Another consequence, which will undoubtedly apply to all mail, will be the fact that "properly coded mail" can be handled more expeditiously. The implica-

tion seems to be that those pieces that do not have the new zip code may be subject to delays in delivery.

For these reasons we earnestly ask all our subscribers and members to inform us as early as possible of their correct new zip. Since our mailing list is not on a scale as large as those of the various news weeklys, we cannot take advantage of the computer tapes that the Postal Service has prepared and will lend to the volume mailers. We will, of course, endeavor to obtain the correct codes; but we would prefer not to have to spend hours on the telephone obtaining the numbers in that way.

That the Postal Service leaves much to be desired, not only in the United States, but abroad as well, was brought home to us with the delivery of our January issue. Second class mailing requirements make it necessary for us to tie securely the various copies of a particular issue going to a particular country in a bundle with a label of the country of destination. Thus, for example, all copies going to Japan will be tied together (in the case of certain countries we have a sufficiently large number of copies to make several bundles and combine them into a "direct sack"). Yet some individuals in each of the "direct sack"-countries received their copies from several weeks to 2 months later than others. We have, of course and unfortunately, no control over these vagaries of the postal services. Our complaints have no effect whatever.

Publication Date of THE VELIGER

THE PUBLICATION DATE of The Veliger is the date printed on the index page; this applies even if the date falls on a legal holiday or on a Saturday or Sunday, days when the U. S. Postal Service does not expedite second class mail matter. That the printed date is the actual date of publication under the rules of the International Commission on Zoological Nomenclature is based on the following facts: 1) The journal is delivered to the Post Office on the first day of each quarter, ready for dispatch; 2) at least three copies are mailed either as first class items or by air mail; 3) about 20 copies are delivered in person to the mail boxes or to the offices of members in the Berkeley area; 4) two copies are delivered to the receiving department of the General Library of the University of California in Berkeley. Thus, our publication is available in the meaning of the Code of the ICZN. The printed publication date, therefore, may be relied upon for purposes of establishing priority of new taxa.

We are willing to accept requests for expediting our journal via AIR MAIL; however, in that case we must ask for an additional payment of US\$8.00 in all cases

where the Veliger goes to domestic addresses, and a deposit of US\$25.00 for all foreign addresses (including PUAS). Of course, we will carry forward as a credit toward the postage charges of the following year any amount over the actually required postage charges.

We think it important to bring to the notice of all our actual and potential correspondents that the postal fee for registered articles is the highest in the world: \$3.25, regardless of destination. Further, to certain countries it is not possible to have mail pieces insured or registered. In the cases where the prospective recipient desires our communications sent as registered article, we must expect advance payment of that fee. We are unable to return manuscripts (either for reworking or with the recommendation that they be submitted elsewhere) other than by ordinary surface mail. In view of the ever more deteriorating postal services in most countries, we can obviously not assume any responsibility for the safe delivery of any items we must dispatch. Our responsibility must and does end with our delivery to the post office of any item.

Sale of C. M. S. Publications:

Effective September 1, 1981, all back volumes still in print, both paper covered and cloth bound, will be available only from "Seashell Treasures Books," 646 30th Street, San Diego, California 92102. The same applies to the supplements still in print, with certain exceptions (see below). Prices of available items may be obtained by applying to Mr. Pisor at the address given above.

Volumes 1 through 8 and 10 through 12 are out of print.

Supplements not available from "Seashell Treasures Books" are as follows:

Supplements to vol. 7 (Glossary) and 15 (Ovulidae) are sold by 'The Shell Cabinet,' P. O. Box 29, Falls Church, VI(rginia) 22046; supplement to vol. 18 (Chitons) is available from 'The Secretary,' Hopkins Marine Station, Pacific Grove, CA(lifornia) 93950.

Supplements

Supplement to Volume 3:

[Part 1: Opisthobranch Mollusks of California
by Prof. Ernst Marcus;

Part 2: The Anaspeidea of California by Prof. R. Beeman,
and The Thecosomata and Gymnosomata of the California Current by Prof. John A. McGowan]

Supplement to Volume 6: out of print.

Supplement to Volume 7: available again; see announcement elsewhere in this issue.

Supplement to Volume 11:

[The Biology of *Acmaea* by Prof. D. P. ABBOTT *et al.*, ed.]
Supplement to Volume 14:

[The Northwest American Tellinidae by Dr. E. V. Coan]
Supplement to Volume 16:

[The Panamic-Galapagan Epitoniidae by Mrs. Helen
DuShane]

[Growth Rates, Depth Preference and Ecological Succession of Some Sessile Marine Invertebrates in Monterey Harbor by Dr. E. C. Haderlie]

Supplement to Volume 17: Our stock of this supplement is exhausted. Copies may be obtained by applying to Dr. E. C. Haderlie, U. S. Naval Post-Graduate School, Monterey, CA (lifornia) 93940.

WE ARE PLEASED to announce that an agreement has been entered into by the California Malacozoological Society, Inc. with Mr. Steven J. Long for the production and sale of microfiche reproductions of all out-of-print editions of the publications of the Society. The microfiches are available as negative films (printed matter appearing white on black background), 105 mm × 148 mm and can be supplied immediately. The following is a list of items now ready:

Volume 1 through Volume 6: \$9.00 each.

Volume 7 through Volume 12: \$12.00 each.

Supplement to Volume 6: \$3.00; to Volume 18: \$6.00
California residents please add the appropriate amount for sales tax to the prices indicated.

Please, send your order, with check payable to Opisthobranch Newsletter, to Mr. Steven J. Long, 359 Roycroft Avenue, Long Beach, California 90814.

Volumes and Supplements not listed as available in microfiche form are still available in original edition from "Seashell Treasures Books," 646 30th Street, San Diego, CA 92102. Orders should be sent directly there.

Single Copies of "The Veliger":

We have on hand some individual copies of earlier issues of our journal and are preparing a list of the various issues available with the prices. Some issues are present in only one or two copies, while others may be present in 10 or more copies. As we are anxious to make room, we will offer these numbers at an exceptionally low price. This list may be obtained by sending a self-addressed, stamped envelope to the Veliger, 1584 Milvia Street, Berkeley, CA (lifornia) 94709. Foreign correspondents should enclose one international postal reply coupon. Requests for the list, for which return postage is not provided, will be ignored.

Membership open to individuals only - no institutional or society memberships. Please send for membership application forms to the Manager or the Editor.

Membership renewals are due on or before April 15 each year. If renewal payments are made after April 15 but before March 15 of the following year, there will be a re-instatement fee of \$1.-. Members whose dues payments (including the re-instatement fee) have not been received by the latter date, will be dropped from the rolls of the Society. They may rejoin by paying a new initiation fee. The volume(s) published during the time a member was in arrears may be purchased, if still available, at the regular full volume price plus applicable handling charges.

Backnumbers of the current volume will be mailed to new subscribers, as well as to those who renew late, on the first postal working day of the month following receipt of the remittance. The same policy applies to new members. THE VELIGER is not available on exchange from the California Malacozoological Society, Inc. Requests for reprints should be addressed directly to the authors concerned. We do not maintain stocks of reprints and also cannot undertake to forward requests for reprints to the author(s) concerned.

WE CALL THE ATTENTION OF OUR

foreign correspondents to the fact that bank drafts or checks on banks other than American banks are subject to a collection charge and that such remittances cannot be accepted as payment in full, unless sufficient overage is provided. Depending on the American banks on which drafts are made, such charges vary from a flat fee of \$1.- to a percentage of the value of the draft, going as high as 33%. Therefore, we recommend either International Postal Money Orders or bank drafts on the Berkeley Branch of First Interstate Bank (formerly United California Bank). This institution has agreed to honor such drafts without charge. UNESCO coupons are NOT acceptable, except as indicated elsewhere in this section.

Regarding UNESCO Coupons

We are unable to accept UNESCO coupons in payment, except at a charge of \$4.25 (to reimburse us for the expenses involved in redeeming them) and at \$0.95 per \$1.- face value of the coupons (the amount that we will receive in exchange for the coupons). We regret that these charges must be passed on to our correspondents; however, our subscription rates and other charges are so low that we are absolutely unable to absorb additional expenses.

Moving?

If your address is changed it will be important to notify us of the new address at least six weeks before the effective date, and not less than six weeks before our regular mailing dates. Because of a number of drastic changes in the regulations affecting second class mailing, there is now a sizeable charge to us on the returned copies as well as for our remailing to the new address. We are forced to ask our members and subscribers for reimbursement of these charges; further, because of increased costs in connection with the new mailing plate, we also must ask for reimbursement of that expense. The following charges must be made:

change of address and re-mailing of a returned issue

— \$2.75 minimum, but not more than actual cost to us.

We must emphasize that these charges cover only our actual expenses and do not include compensation for the extra work involved in re-packing and re-mailing returned copies.

Policy Regarding Reprints

It seems necessary to bring the following points to the notice of prospective authors:

All manuscripts submitted for inclusion in *The Veliger* are subject to review by at least two scientists; acceptance is entirely on the basis of merit of the manuscript. Although many scientific journals assess page charges, the Executive Board of our Society, for the time being at least, wishes to avoid this possible financial handicap to the younger contributors. However, because of the high cost of halftone plates, a suitable contribution to reimburse the Society must be sought.

Similarly, while it was hoped at the "birth" of *The Veliger*, that a modest number of reprints could be supplied to authors free of charge, this has not as yet become possible. We supply reprints at cost. Unfortunately, in recent years it has become "fashionable" for some authors and some institutions to ignore paying for reprints ordered and supplied in good faith or to delay payment for a year or more. This causes financial losses to the Society since our debts are paid promptly. Since the Society is in fact not making any profit, it is necessary to introduce

a policy which, it is hoped, will protect us against negligence or possible dishonesty. In the case of manuscripts from sources outside of the United States, if a manuscript is accepted, we will inform the author of the estimated cost of reprints and require a deposit in U. S. funds to cover these costs. If such a deposit is not made, we will not supply any reprints. In the case of non-payment by domestic authors or institutions, we will pursue legal recourses.

To Prospective Authors

Postal Service seems to have deteriorated in many other countries as well as in the United States of America. Since we will absolutely not publish a paper unless the galley proofs have been corrected and returned by the authors, the slow surface mail service (a minimum of 6 weeks from European countries, 8 to 12 weeks from India and Africa) may make a delay in publication inevitable. We strongly urge that authors who have submitted papers to *The Veliger* make all necessary arrangements for expeditious reading of the proofs when received (we mail all proofs by air mail) and their prompt return by air mail also.

Since we conscientiously reply to all letters we actually receive, and since we experience a constant loss in insured and registered mail pieces, we have come to the conclusion that if a correspondent does not receive an answer from us, this is due to the loss of either the inquiry or the reply. We have adopted the habit of repeating our inquiries if we do not receive a reply within a reasonable time; that is, 6 weeks longer than fairly normal postal service might be expected to accomplish the routine work. But we can not reply if we have never received the inquiry.

Because of some distressing experiences with the Postal Service in recent years, we now urge authors who wish to submit manuscripts to our journal to mail them as insured parcels, with insurance high enough to cover the complete replacement costs. Authors must be prepared to document these costs. If the replacement costs exceed \$400.-, the manuscript should be sent by registered mail with additional insurance coverage (the maximum limit of insurance on parcel post is, at present, \$400.-). We are unable to advise prospective authors in foreign countries and would urge them to make the necessary inquiries at their local post offices.

We wish to remind prospective authors that we have announced some time ago that we will not acknowledge the receipt of a manuscript unless a self-addressed stamped envelope is enclosed (two International Postal Reply Coupons are required from addresses outside the U. S. A.). If correspondence is needed pertaining to a manu-

script, we must expect prompt replies. If a manuscript is withdrawn by the author, sufficient postage for return by certified mail within the U.S.A. and by registered mail to other countries must be provided. We regret that we must insist on these conditions; however, the exorbitant increases in postal charges leave us no other choice.

Some recent experiences induce us to emphasize that manuscripts must be in final form when they are submitted to us. Corrections in galley proofs, other than errors of editor or typographer, must and will be charged to the author. Such changes may be apparently very simple, yet may require extensive resetting of many lines or even entire paragraphs. Also we wish to stress that the requirement that all matter be double spaced, in easily legible form (not using exhausted typewriter ribbons!) applies to all portions of the manuscript – including figure explanations and the “Literature Cited” section.

It may seem inappropriate to mention here, but again recent experience indicates the advisability of doing so: when writing to us, make absolutely certain that the correct amount of postage is affixed and that a correct return address is given. The postal service will not forward mail pieces with insufficient postage and, if no return address is given, the piece will go to the “dead letter” office; in other words, it is destroyed.

Endowment Fund

In the face of continuous rises in the costs of printing and labor, the income from the Endowment Fund would materially aid in avoiding the need for repeated upward adjustments of the membership dues of the Society. It is the stated aim of the Society to disseminate new information in the field of malacology and conchology as widely as possible at the lowest cost possible.

General Notice

Because of an increasing number of strange occurrences your editor deems it important to clarify our policy with respect to correspondence.

1. We never reply to letters that do not reach us. Since the U. S. postal service no longer forwards mail pieces that are not franked properly, correspondents waiting for our reply might consider the possibility that their letter falls into this category.
2. We do not acknowledge the receipt of a manuscript unless a self-addressed, stamped envelope is enclosed.
3. We do not reply to complaints regarding the non-arrival of our journal, if these complaints are made at a time when the claimed issue could not possibly have reached its destination. In view of the poor postal service throughout the world, it is unrealistic to expect, for example, the July issue in a shorter period than from 2 to 3 weeks in the United States, in less than 4 to 6 weeks in Europe, and in less than 2 to 4 months in other areas of the world; South American countries, in particular, have to expect maximum delays. It should be obvious that we are not responsible for the postal service.
4. We particularly object to complaints about non-receipt of issues which are scheduled to be published as much as 6 months after the complaint was sent! A little consideration of what is possible and what is absurd should help to obviate such untimely complaints.
5. We are receiving an increasing number of requests for our list of individual back numbers that are still available, as well as for our suggestions to prospective authors. These requests state that a self-addressed stamped envelope is enclosed — but somehow the writer must have forgotten to do so. These requests also are not answered by us.

We consider that our policy is justified for several reasons: the requirement for self-addressed, stamped envelopes has been stated in every issue of the Veliger for the past several years. Since we are a non-profit organization, we prefer to reserve our energy and our resources for productive purposes. However, we do conscientiously, and usually exhaustively, reply to all correspondence that we consider legitimate. Moreover, such correspondence is usually answered the same day as received, with the reply posted the next morning at the main post office in Berkeley. What happens afterwards is beyond our control.

BOOKS, PERIODICALS, PAMPHLETS

We regret that compelling reasons prevented us from presenting any of the book reviews or announcements of articles that had appeared in the months preceding our January issue. We are endeavoring to remedy that omission as best as we are able to do so.

The Pelecypod Family Cardiidae: A Taxonomic Summary

by A. MYRA KEEN. Tulane Studies in Geology and Paleontology 16 (1): 40 pp.; 13 pls. (17 September 1980)

This important, long-awaited paper culminates some 45 years of study of this family by Dr. Keen. She discusses the generic-level taxa in the family, allocating them to six subfamilies. The generic taxa are illustrated, and keys to them are provided. The evolution and the geographic distribution of units of the family, which arose in the late Triassic, are discussed. Some notes on Édouard Fischer-Piette's 1977 review of the family are given.

Dr. Keen has sufficient extra copies of the paper to handle reprint requests (2241 Hanover Street, Palo Alto, CA (lifornia) 94306).

Eugene V. Coan

Malacological Review

P. O. Box 420, Whitmore Lake, Michigan, 48189, U.S.A.
vol. 14 (1-2): iv+202 pp.; illust. 1981

This latest issue of the Malacological Review, like its 13 predecessors, contains original articles and brief notes. However, 46 pages are devoted to what may be called a "historical recapitulation" of the contents pages of the American Malacological Union up to the time that Malacological Review started to appear.

We have expressed our astonishment at the modest price of this publication on previous occasions and we do it again, even though, forced by ever increasing costs of production and of postage rates, the subscription rate had to be increased effective with the present volume.

We know of no other publication that keeps its readers abreast of publications in all fields of malacology as does this annual publication. The active researcher can scan rapidly the reproduced tables of contents of 27 periodicals

from a dozen different countries to find articles possibly pertinent to his own research interest. From there, the actual article can then be pursued.

R. Stohler

The Audubon Society Field Guide to North American Seashells

by HARALD A. REHDER. 894 pp. of which 235 pp. contain 3 color reproductions of shells each. Alfred A. Knopf, New York. \$11.95 (21 August 1981)

This is a superb addition to the Audubon Society's series of field guides. One flaw — if it is a flaw — is introduced by giving every molluscan species a "common" name, which frequently is nothing other than a relatively free translation of the scientific name. This, we think, is due to the fact that the earliest field guides were produced for bird watchers. Common names for birds have been in use for a long time; we question, however, the artificial creation of common names where none exist while we would applaud the listing of all common names given by inhabitants of the various parts of the world to a particular species. We remember the famous work of Naumann, Die Vögel Mitteleuropa's, where sometimes a list of 20 or 30 different "common" names were listed. Our remarks are most certainly not meant to detract from the great value of this book nor is it intended in the slightest as a reproof to Dr. Rehder, who really deserves the warmest commendations for a well prepared, well organized book that will be welcomed by many shell collectors here and abroad.

We think that in keeping with the well-known attitude of the Audubon Society toward protection of Nature, this guide is intended to encourage "seeing" rather than "collecting" shells. There is an index with fair-sized circles in front of the common names to make it easy for the user to check off the species seen. Any attempt to encourage preservation deserves our support.

R. Stohler

The Tribe Alasmidontini (Unionidae: Anodontinae), Part I: *Pegias*, *Alasmidonta*, and *Arcidens*

by ARTHUR H. CLARKE. Smithsonian Contributions to Zoology. No. 326: pp. 1-101; 32 illustrations (maps, diagrams, drawings and SEM micrographs).

The author recognizes 14 species in the three genera enumerated in the title. The account of each species is

organized as follows: the accepted (valid) name is followed by a detailed synonymy; subheadings are: the shell; topographic anatomy; glochidium; life history; geographical records; and in some instances, remarks.

The illustrations are clear and illustrate well some of the finer details, especially of the glochidia. These larvae typical of freshwater clams, adapted to a transitory parasitic existence on fish, reveal fierce looking armature which enables them to attach to the slippery skin of their host. Those of us who have studied glochidia only under the light microscope (as this reviewer did) are certainly impressed by this equipment of the larva.

R. Stohler

**Functional Morphology and Development
of Veliger Larvae of the European Oyster,
Ostrea edulis Linné**

by THOMAS R. WALLER. Smithsonian Contributions to Zoology. No. 328: pp. 1 - 70; 152 figures, predominantly SEM micrographs.

Another superb, scholarly contribution from this author. Through the skillful application of modern research methods many structures and patterns heretofore either unknown or only poorly understood were observed. To quote the most important results from the abstract:

"(1) the presence of four ciliary bands on the velum, not three; (2) the heel-first development of the foot, with medial ciliation of the toe preceding complete ciliation; (3) the order of appearance and structure of major duct openings on the foot and body wall; (4) the beginning of larval eyes as hemispherical tufts of elongate microvilli; (5) the early development of gill primordia; and (6) the early appearance of a prominent gill bridge, which originates by cross-contact of cilia on the mantle margins of epithelial cells and tissue fusion."

The illustrations are clear and well reproduced, aiding the reader in understanding what Dr. Waller presents in the clearly written text.

R. Stohler

**The Family Buccinidae Part 1:
The Genera *Nassaria*, *Trojana* and *Neoterion***

by WALTER O. CERNOHORSKY. Monographs of Marine Mollusca, No. 2: 52 pp.; 42 halftone figures (called plates). American Malacologists, Inc. (15 August 1981)

This is the type of carefully documented and well illustrated work we are accustomed to see produced by this author. The format is the same as that of "Indo-Pacific Mollusca" and is aimed at the same audience as that publication.

R. Stohler

Guide to the Nudibranchs of California

by GARY R. McDONALD & JAMES W. NYBAKKEN. Revised edition (see the review of the same work by Eugene Coan on p. 84 of this volume).

This is not a revision in the strict sense since a perusing of the text reveals no differences from the original issue. However, the colored illustrations, for the most part, are vastly improved. No corrections of the taxonomic inadequacies pointed up by the reviewer have been attempted.

R. Stohler

**Canadian West Coast Flying Squid
Experimental Fishery**

by F. R. BERNARD. Department of Fisheries and Oceans Resource Services Branch, Pacific Biological Station, Nanaimo, British Columbia V9R 5K6. Report No. 122: 6 pp. text; 5 tables; 3 maps; 1 graph. April 1981

In the summer of 1980, an experimental drift net fishery was undertaken for *Ommastrephes bertramii* on the high seas off the west coast of Vancouver Island. The conclusion reached in this report is that commercial fisheries for this squid species is not promising because of the requirements for large-sized vessels and the absence of shore-based processing facilities.

R. Stohler

***Platypleuroceras nodosum* (Futterer) (Ammonoidea)
aus dem Unter-Pliensbachium SW-Deutschlands**

by RUDOLF SCHLATTER. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) Nr. 46: 11 pp.; 1 plt.; 4 text figs. 15 December 1979

The species mentioned in the title is described in more detail than has been available until now; a neotype, in the collection of the Bayerische Staatsammlung für Palä-

ontology und Historische Geologie in Munich, is designated.

R. Stohler

**Revision der Ceratiten aus der *atavus*-Zone
(Oberer Muschelkalk, Oberanis)
von SW-Deutschland**

by MAX URLICHS & RUDOLF MUNDLOS. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) Nr. 48: 42 pp.; 4 pls.; 7 text figs. 1 January 1980

Several species of this group are reviewed and closely related species are redescribed for purposes of comparison. One subspecies is renamed: *Paraceratites* (*Progonoceratites*) *flexuosus bussei*, a new name for *Ceratites flexuosus* var. *crassa* Riedel, 1918.

R. Stohler

**Die Ammoniten-Gattung *Caumontisphinctes*
aus dem südwestdeutschen Subfurcaten-Oolith
(Bajocium, Mittl. Jura)**

by GERARD DIETL. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) Nr. 51: 43 pp.; 5 pls.; 5 text figs. 15 January 1980

On the basis of systematical collecting, 13 species of *Caumontisphinctes* could be documented and 1 species and 1 new subspecies are described.

R. Stohler

**Über die „sowerbyi-Zone“ (= *laeviuscula*-Zone, Unter-Bajocium, Mittl. Jura) in einem Profil bei Nenningen
(östl. Schwäb. Alb)**

by GERD DIETL & WILLI HAAG. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) Nr. 60: 11 pp.; 1 plt.; 1 text fig. 1 December 1980

Erstfund eines Orthoceratiden (*Michelinoceras campanile*) im germanischen Muschelkalk

by MAX URLICHS & WOLFGANG SCHRÖDER. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) Nr. 59: 7 pp.; 1 plt.; 3 text figs. 15 Dec. 1980

The species listed in the title has been found for the first time in Germany; it was known before this from Turkey and Jugoslavia only.

R. Stohler

**Die Ammoniten-Gattung *Leptosphinctes* aus dem
südwestdeutschen Subfurcaten-Oolith
(Bajocium, Mittl. Jura)**

by GERD DIETL. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) Nr. 66: 49 pp.; 10 pls.; 7 text figs. 15 December 1980

Based on a systematical collecting of ammonites, 18 species of the genus *Leptosphinctes* and their stratigraphic distribution were documented. *Leptosphinctes* (*Cleistosphinctes*) *killertalensis* and *L. (C.) minor* are described as new species.

R. Stohler

**Biostratigraphie und Ammonitenfauna
des Unter-Pliensbachium im Typusgebiet
(Pliensbach, Holzmaden und Nürtingen,
Württemberg, SW-Deutschland)**

by RUDOLF SCHLATTER. Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) Nr. 65: 261 pp.; 23 pls.; 15 text figs.; 2 tables and 25 "Beilagen" (groups of schematic drawings). 31 December 1980

This extensive study, based on ca. 2400 ammonites, resulted in a better understanding of the strata mentioned in the title. The holotype of *Platypleuroceras brevispina* is described in detail for the first time; lectotypes are designated for several species originally described by Oppel, d'Orbigny, or Quenstedt. A new subgenus and a new species are described as well as one species renamed.

R. Stohler

THE VELIGER is open to original papers pertaining to any problem concerned with mollusks.

This is meant to make facilities available for publication of original articles from a wide field of endeavor. Papers dealing with anatomical, cytological, distributional, ecological, histological, morphological, physiological, taxonomic, etc., aspects of marine, freshwater or terrestrial mollusks from any region, will be considered. Even topics only indirectly concerned with mollusks may be acceptable. In the unlikely event that space considerations make limitations necessary, papers dealing with mollusks from the Pacific region will be given priority. However, in this case the term "Pacific region" is to be most liberally interpreted.

It is the editorial policy to preserve the individualistic writing style of the author; therefore any editorial changes in a manuscript will be submitted to the author for his approval, before going to press.

Short articles containing descriptions of new species or lesser taxa will be given preferential treatment in the speed of publication provided that arrangements have been made by the author for depositing the holotype with a recognized public Museum. Museum numbers of the type specimens must be included in the manuscript. Type localities must be defined as accurately as possible, with geographical longitudes and latitudes added.

Short original papers, not exceeding 500 words, will be published in the column "NOTES & NEWS"; in this column will also appear notices of meetings of the American Malacological Union, as well as news items which are deemed of interest to our subscribers in general. Articles on "METHODS & TECHNIQUES" will be considered for publication in another column, provided that the information is complete and techniques and methods are capable of duplication by anyone carefully following the description given. Such articles should be mainly original and deal with collecting, preparing, maintaining, studying, photographing, etc., of mollusks or other invertebrates. A third column, entitled "INFORMATION DESK," will contain articles dealing with any problem pertaining to collecting, identifying, etc., in short, problems encountered by our readers. In contrast to other contributions, articles in this column do not necessarily contain new and original materials. Questions to the editor, which can be answered in this column, are invited. The column "BOOKS, PERIODICALS, PAMPHLETS" will attempt to bring reviews of new publications to the attention of our readers. Also, new timely articles may be listed by title only, if this is deemed expedient.

Manuscripts should be typed in final form on a high grade white paper, 8½" by 11", double spaced and accompanied by a carbon copy.

A pamphlet with detailed suggestions for preparing manuscripts intended for publication in **THE VELIGER** is available to authors upon request. A self-addressed envelope, sufficiently large to accommodate the pamphlet (which measures 5½" by 8½"), with double first class postage, should be sent with the request to the Editor.

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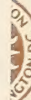
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